Mem. Qd Mus. **20**(2): 319–49, pls. 1–2. [1981]

MUTTABURRASAURUS, A NEW IGUANODONTID (ORNITHISCHIA: ORNITHOPODA) DINOSAUR FROM THE LOWER CRETACEOUS OF QUEENSLAND

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ABSTRACT

A partial skeleton of an iguanodontid ornithopod has been recovered from the Mackunda Fm. (Albian) on the Thomson River near Muttaburra, central Queensland. This material is referred to *Muttaburrasaurus langdoni*, gen. et sp. nov. This new iguanodontid is characterized by an inflated, hollow muzzle; maxillary teeth lacking any central carina; a low, broad skull; anterior caudal centra with ventral excavations; four metatarsals, and; an apparent articulation of the fibula with the astragalus.

INTRODUCTION

Dinosaur remains are uncommon in Australian deposits. Of those discovered, by far the greatest number have been from Queensland. Excluding footprints, widely known in Queensland and elsewhere, the majority of records involving actual bone remains are from the freshwater and shallow marine sediments of the Great Artesian Basin, which cover much of the state. Described remains have been of partial skeletons and isolated bones and in recent years, field investigations in the freshwater sediments of the Winton Formation have yielded fragmentary skeletons of sauropods. Some of this work was undertaken independently by the Queensland Museum, while part was in conjunction with the American Museum of Natural History.

Among earlier collected material the most completely known species, described by Longman (1926, 1927), is the sauropod *Rhoetosaurus brownei* from the freshwater Injune Creek Beds of Middle Jurassic age on "Taloona" Station. Recent investigations of the site confirmed the presence of additional material which was apparently *in situ*. Study of these remains, still lacking cranial material, will add considerably to knowledge of this animal.

Dinosaur bones have also been recorded from the Wilgunya Sub-Group (especially the Toolebuc Limestone) of Lower Cretaceous (Albian) age, associated with a rich, shallow water, marine invertebrate fauna and a broad suite of marine vertebrates including fish and marine reptiles. The only described dinosaur material is another large sauropod, *Austrosaurus mckillopi* Longman (1933) recovered from 'Clutha' Station, near Maxwelton, central Queensland. The material comprises a series of dorsal vertebrae and part of a rib. An isolated, partial cervical vertebra(QM F6142) from a very large sauropod is also known from the Wilgunya Sub-Group.

Other described remains from Australia are based on even less material than *Austrosaurus*. Seeley (1891) recorded the presence of *Agrosaurus macgillivrayi* from isolated bones from unrecorded sediments, probably of Triassic age, from the coast of North Queensland. A series of opalized specimens from the Cretaceous sediments at Lightning Ridge, northern New South Wales was described by Huene (1932). These comprised a theropod tooth, a theropod caudul vertebra *Walgettosuchus woodwardi*, a femur described as *Fulgurotherium australe* and a theropod metacarpal described as *Rapator ornitholestoides*. These have recently been reviewed by Molnar (1980), who also reported hypsilophondontid material from the Ridge. Recently isolated theropod and hypsilophodontid material has also been discovered on the Victorian coast, near Cape Paterson and Cape Otway.

The material considered in the present study represents the most completely known dinosaur yet discovered from Australia. Its location was brought to the notice of the Queensland Museum in 1963 by a grazier, Mr D. Langdon, of Muttaburra, central Queensland. The specimen was exposed within a cattle holding area on the banks of the Thomson River, near Muttaburra. Unfortunately, it had been somewhat scattered by stock over the years and some had been collected by local residents before recovery could be organized. However, recognizing the importance of the find, residents returned much of the removed material and it is believed that no major elements originally preserved now remain in private hands. The discovery was previously recorded by Bartholomai (1966) and Hill, Playford and Woods (1968).

Preparation and reassociation of the parts of the specimen have been achieved with considerable difficulty, using a combination of mechanical and acetic acid techniques and jig-saw puzzle approach. Although limited further detail will be forthcoming with continued preparation, the authors believe that further delay in its description is unwarranted.

The assistance of the Myer Foundation in awarding a Travel Grant to the senior author, in part to enable comparative studies to be undertaken in England and France, is gratefully acknowledged. Mr M. Tanimoto drew our attention to published photographs of *Probactrosaurus*, for which we are grateful.

We would also like to thank Margaret Oakden for her restoration, and Dianne Ashwell for typing the drafts of the ms.

Order ORNITHISCHIA Seeley
Suborder ORNITHOPODA Marsh
Family Iguanodontidae Cope
Genus *Muttaburrasaurus* nov.

TYPE SPECIES: *Muttaburrasaurus langdoni* nov.

DIAGNOSIS: Large iguanodontid with nasal region of snout inflated; maxillary teeth with multiple low ridges but lacking central carina; postorbital region of skull broad and low; quadrate inclined posteriorly; lateral process present on frontal; dorsal centra keeled; anterior caudal centra with ventral pits; four metatarsals present. A differential diagnosis will be presented with the comparison with other ornithopods.

ETYMOLOGY: Derived from Muttaburra, the name of the township in central Queensland near the type locality, and *sauros*, Latin, used in the sense of reptile or saurian.

SPECIES: *Muttaburrasaurus langdoni* nov.

TYPE SPECIMEN:
Queensland Museum F6140, a nearly complete skeleton, lacking most of the tail. This material includes the phalanges previously numbered F6095 (figured in Hill, Playford and Woods, 1968).

LOCALITY: The banks of the Rock Hole, Thomson River, on "Rosebery Downs" Station, approximately 4½ km southeast of Muttaburra, central Queensland, at M.R. 242175 Muttaburra 4-mile series (approximately M.R. 245165 on the Muttaburra 1:250000 series).

HORIZON: Mackunda Fm.

AGE: Albian (Vine and Day, 1965).

ETYMOLOGY: The specific name honours Mr. D. Langdon, of Muttaburra, who discovered the specimen, and reported it to the Queensland Museum.

DIAGNOSIS: As only a single species is attributed to this genus, the specific diagnosis necessarily cannot be separated from that of the genus.

The bones were partially exposed by weathering in a calcareous mudstone concretion (or series of concretions) which had been exposed on the surface being harder than the containing sediment. Nearby concretionary structures contained a rich suite of shallow water marine pelecypods, gastropods and rare ammonites.

It is clear that the holotype and the invertebrates were recovered from the Mackunda Formation, within the Manuka Sub-Group, regarded by Vine *et al.* (1967) and Vine and Day (1965) as being of Lower Cretaceous (Albian) age. The dinosaur thus adds to the known fossil record of the Tambo Faunal Division. Vine and Day (1965) regard the argillaceous and arenaceous sediments of the Mackunda Formation as having been deposited in marine and paralic environments. Because of the close association of the dinosaur remains with non-abraded shallow-water marine molluscs, it is believed that the specimen was preserved some distance from the Albian shoreline, away from the influence of heavy wave action. It is assumed that the carcase floated out to sea, sank and was interred within the marine muds.

DESCRIPTION

THE SKULL

The skull is preserved in a slightly distorted and crushed condition. Some shedding and bone loss has occurred, particularly posterodorsally, anteriorly and on the right side. Only the posterior portions of the mandibles are known. However, most major external bone elements are represented, particularly from the left side. Matrix masks much of the ventral surface, although elements are occasionally seen in section along fortuitous cracks. The skull is illustrated in its existing state in Plate 1, and Fig. 1 while Fig. 2 shows the reconstructed skull.

Several notable features of the skull stand out. The postorbital region of the skull is low and broad, even accounting for its incompleteness dorsally. In height this region is slightly over half its maximum breadth. The anterior portion of the snout as preserved is greatly inflated into an apparently hollow bulla, giving the skull a unique appearance unlike that of any other described form. This structure will be described in greater detail with the discussion of the nasal and premaxillary bones. The foramen magnum is not circular or elliptical in form, but has the peculiar appearance of being in form like a large semicircle joined to a small one of about half its radius (Fig. 1). The bar posteriorly bounding the infratemporal fenestra is remarkable for its anteroposterior breadth.

SUPRAOCCIPITAL. The supraoccipital forms most of the dorsal roof of the foramen magnum. It is mainly known from its external, posterior aspect, the surface of which is inclined very slightly anteriorly. The ventral one-third is weakly concave transversely, while the dorsal two-thirds bears a strong, narrow, median ridge separating deep, lateral concavities for *M. spinalis capitis*. The surface immediately below the ridge is transversely concave and carries a deep, narrow groove leading to a small foramen on each side of the midline. The bone is extended laterally into

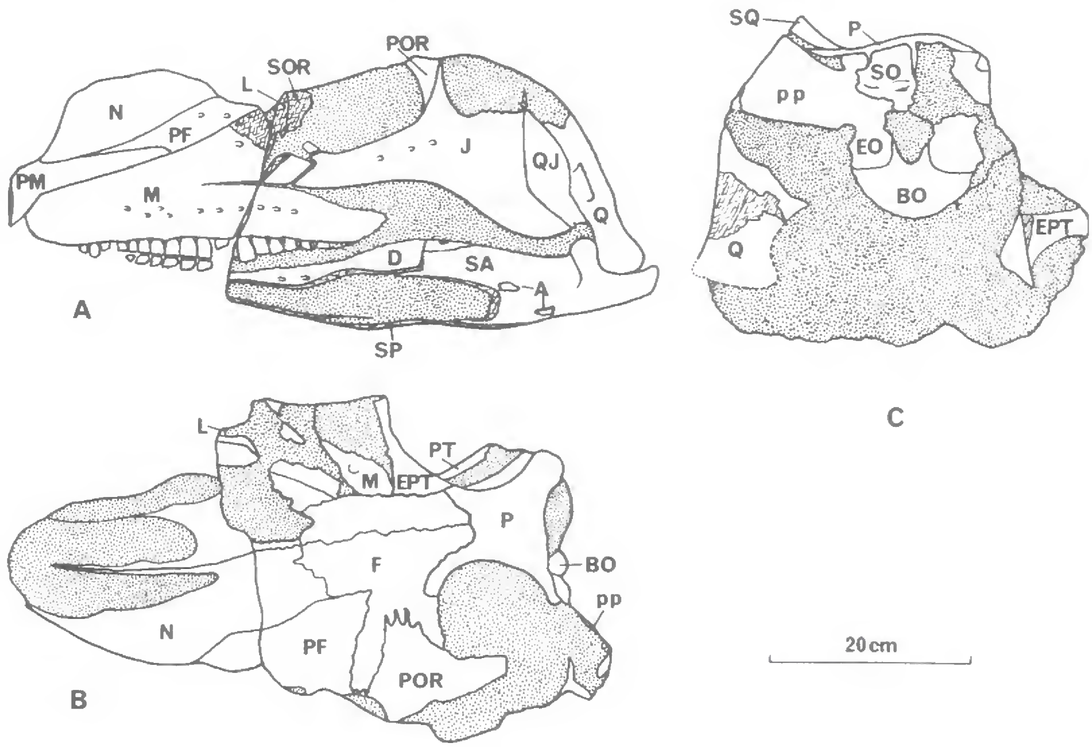

FIG. 1. The skull and jaws of *Muttaburrasaurus langdoni* (QM F6140) as preserved. A, lateral view; B, dorsal view; C, posterior view. Abbrev.: A, angular; BO, basioccipital; D, dentary; EO, exoccipital; EPT, ectopterygoid; F, frontal; J, jugal; L, lacrimal; M, maxilla; N, nasal; P, parietal; PF, prefrontal; PM premaxilla; POR, postorbital; pp, paroccipital process; PT, pterygoid; Q, quadrate; QJ, quadratojugal; SA, surangular; SO, supraoccipital; SOR, supraorbital; SQ, squamosal. The stipple represents matrix, and the hatching broken surfaces.

leaf-shaped borders. The superior rim of the foramen magnum is broadly concave transversely and is angled obliquely anterodorsally. A weak, median, ventral process is present extending into the foramen magnum.

Sutural relationships with the exoccipital-opisthotic are difficult to interpret but traces suggest the limits to the bones. Relationships of the supraoccipital and proötic are largely obscured.

Near the ventrolateral border with the paroccipital process, a shallow transverse groove leads to the centre of the posterior surface and is defined dorsally by a very small, posteriorly directed process.

EXOCCIPITAL AND OPISTHOTIC. Sutural relationships between the exoccipital and opisthotic are difficult to interpret. They combine to make up the bulk of the lateral and dorsolateral margins of the foramen magnum and ascend as a stout pillar from the upper limit of the occipital condyle to obliquely meet the supraoccipital. A short posteromedial process forms the dorsolateral margin of the foramen magnum. The surface is deeply concave and the bones continue posterolaterally into a broad, flaring, paroccipital process. A shallow depression is present immediately lateral to the margin of the foramen magnum. Dorsally, a stout buttress from the paroccipital process supports the parietal and laterally this process supports the squamosal. Posteriorly the paroccipital process is gently convex dorsoventrally but is planar anteriorly. Lateral aspects of the cranial base are only partly visible. A large foramen, presumably for the hypoglossal n., is present anterolaterally in the ascending pillar close to the basioccipital.

BASIOCCIPITAL. The basioccipital forms the occipital condyle and the ventral and ventrolateral margins of the foramen magnum. The condyle is well developed, rounded and produced ventrally as well as posteriorly. Other surfaces are masked by matrix.

PROÖTIC AND BASISPHENOID. The proötic is partially exposed on the right side, sufficient to observe part of its articulation with the parietal

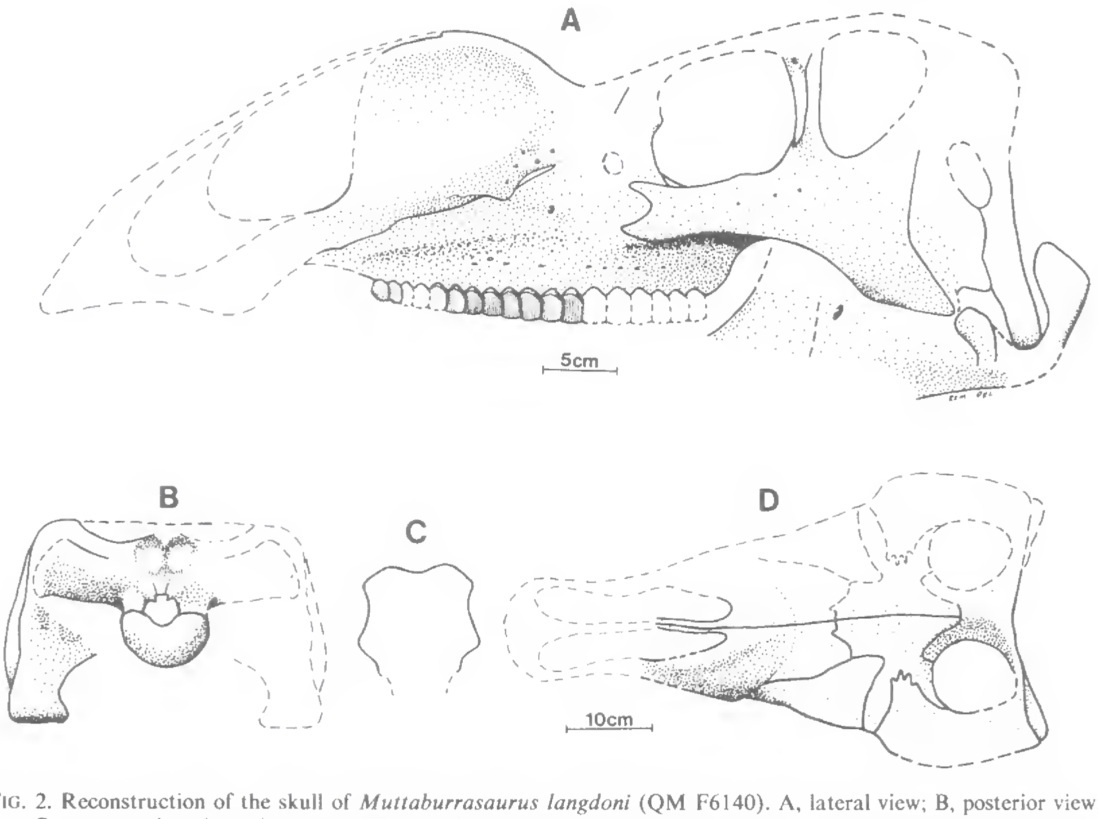

FIG. 2. Reconstruction of the skull of *Muttaburrasaurus langdoni* (QM F6140). A, lateral view; B, posterior view; C, cross-section through nasal bulla just behind posterior extremity of nares; D, dorsal view. Reconstructed portions dashed, right side of skull based on left, cranial roof region based on those portions of the roofing elements preserved, and anterior portion of snout reconstructed by analogy with *Iguanodon mantelli*.

but insufficient for description. The basisphenoid is masked by matrix.

PARASPHENOID. This bone is largely covered by matrix. A fortuitous break across the skull exposes in section what probably is the parasphenoid. It appears as a small, anteriorly directed process, V-shaped in section, with the dorsal arms slightly directed mesially and containing a very deep, dorsal concavity (PL. 2, B). A very deep, extremely thin flange of bone extends ventrally at the mid-line. This flange is deeper in this section than the main body of the bone.

LATEROSPHENOID. The laterosphenoid is too poorly exposed for description.

ORBITOSPHENOID. If preserved, the orbitosphenoid is still masked by matrix.

PREMAXILLA. The premaxilla is incomplete anteriorly and dorsally and little remains of the edentulous portion. It was relatively large and was expanded anteriorly both transversely and dorsoventrally. Posteriorly, it is produced into a relatively short, thin, flat process between the maxilla and nasal. Dorsomesially, the premaxilla is concave and floors the nasal passage. It is sharply excavated ventromesially with a sharply crested, free ventrolateral border produced to about the same level as, or slightly dorsal to, the anterior margin of the maxillary dentition. Remnants remain of the median dorsal process contributing to the anterior and dorsal aspects of the naris. The ventrolateral margin remaining is rugose, suggesting the presence of a horny sheath.

MAXILLA. The maxilla is known both laterally and in section but mesial aspects are masked by matrix. The bone is elongate and anteriorly is dorsoventrally shallow but is much deeper posteriorly. The lateral margin is longitudinally shallowly concave anteriorly, near planar above the mid-cheek area and markedly concave below the orbit. A series of foramina are present, irregularly placed anteriorly but becoming more regular in a single series posteriorly, slightly above the mid-line of this part of the bone. All are directed posteriorly and probably transmitted nerves and blood vessels to the cheeks (cf. Galton, 1973a).

The maxilla bears a minimum of 18 functional, socketed teeth. Anterior to the first tooth, is an edentulous section extending a short distance to butt against the ventrolaterally directed expansion of the premaxilla. Internally, the ventral part of the bone is a robust, longitudinally orientated rod with the convexity directed slightly dorsomesially. The lateral margin above the foramina is relatively thin and the foramina appear to open into a broad, transversely concave, channel-like shelf.

Immediately above the main body of the maxilla, the bone is flexed along a longitudinal axis, the angular relationship being emphasized by dorsoventral crushing. A tongue-like extension of the maxilla joins the anterodorsal surface of the jugal. Dorsally, the maxilla broadly contacts the nasal and anterodorsally it contacts the premaxilla. Posterodorsally, it appears excluded from contact with the prefrontal but contacts the lacrymal posteriorly and posterodorsally. In this area it surrounds the posteroventral, ventral and anteroventral margins of the small antorbital fenestra. The dorsal part of the maxilla is sharply concave anteriorly and slightly sinuous across its greatest height.

NASAL. The nasal is a relatively thin bone, widely expanded dorsally into a bizarre, bulbous structure which, allowing for slight dorsoventral crushing of the skull, was higher than the cranial roof. Loss of bone has occurred anterodorsally and the nasal opening was apparently relatively large, ovate and directed dorsoanterolaterally. Contact with the premaxilla is short laterally, and posteriorly it joins the prefrontal and frontal. The bulk of the ventral contact is with the maxilla, although minor contact with the lacrymal is present posteriorly. The bulbous expansion is longitudinally sinuous laterally. In a dorsoventral section, it is shallowly concave laterally. A series of small foramina are present posteroventrally. The anterior and dorsal edges contribute to the dorsomesial and lateral borders of the naris.

LACRYMAL. The lacrymal is not well preserved on either side. Sufficient remains to indicate that it was a relatively small but comparatively thick bone wedged between the maxilla, jugal, prefrontal and supraorbital. The lacrymal forms part of the anterior margin of the orbit and contributes to the anterodorsal, dorsal and posterodorsal margins of the antorbital fenestra. The lacrymal duct is directed through the dorsal body of the bone.

PREFRONTAL. The prefrontal is a large bone positioned between the frontal, nasal, lacrymal and supraorbital. Its anteroventral margin is truncate, giving a broad contact with the posterolateral margin of the nasal, while its posterior margins expand and contribute to the skull roof and the bulk of the anterodorsal orbital margin. It widely excludes the frontal from much of the orbital margin. The dorsal surface is flattened.

SUPRAORBITAL. The supraorbital is incomplete posteriorly. Shedding and fracturing have largely obscured its surface features. It is a small element at the anterodorsal orbital margin and making wide contact with the prefrontal and lacrimal. Posteriorly it probably parallelled the dorsal orbital margin.

POSTORBITAL. This is a triradiate element, sharp edged and forming the posterodorsal and part of the posterior orbital margins and the anterolateral portion of the upper temporal bar. The bone is damaged dorsally and posteriorly but it was flattened dorsally. The posterior process tapers away from the body of the bone, while the ventral process is elongate and tapers along the anterior surface of the ascending process of the jugal. A circular depression, with rugose posterior and dorsal rim, containing a foramen is present towards the top of the ventral process. Contact mesially is with the parietal and frontal and anteriorly with the frontal, which it excludes from major contribution to the dorsal orbital margin.

PTERYGOID. The pterygoid is largely masked by matrix and only the broad right alar process for the quadrate is exposed.

ECTOPTERYGOID. The ectopterygoid is exposed only on the right side and from above. It has been somewhat damaged by fracturing. The main portion consists of a stout bar, subtriangular in section, which continues mesially into a widely expanded plate, the expansion being greatest posteroventrally. The anterior surface of the bar contacts the mesial portion of the posterior surface of the maxilla, while the bar is slightly expanded laterally near its junction with the jugal. The mesial flared section is subtriangular with the apex directed dorsally and with the bone thinning anteriorly and posteriorly. It broadly contacts the pterygoid.

PALATINE AND VOMER. These bones are masked by matrix but a portion of a bone interpreted as palatine is visible from above in the right orbital area.

FRONTAL. The frontal is a large, elongate bone contributing minimally to the dorsal orbital margin and forming a large proportion of the dorsal skull roof. Considerable shedding has occurred but sutures may still be interpreted. The frontal is nearly planar anteroposteriorly and transversely, contributing to the rather flat skull roof.

PARIETAL. The parietal has suffered shedding dorsally and along the occipital crest. It is a large element in dorsal aspect, extending anterior the supratemporal fenestrae. The bone contributes to the anterodorsal and mesial margins of the supratemporal fenestra, and contacts the frontal. From above the surface is flattened on its lateral portion but mesially it is weakly crested between the supratemporal fenestrae. A strong occipital crest is also formed posteriorly where it extends above and well posterior to the supraoccipital plane. Transversely, the dorsal margin of the occipital crest is strongly convex. Lateral margins of the crest are supported by stout buttresses from the paroccipital processes. Posteroventrally, the bone contacts the squamosal and laterally contacts the laterosphenoid, supraoccipital and postorbital within the supratemporal vacuity.

JUGAL. The jugal is a large bone contributing to the ventral moiety of the infratemporal fenestra and to the posteroventral margin of the skull. Its ventral margin is concave. The outer orbital margin is gently rounded and a shelf of the jugal extends mesially to contribute to the floor of the orbit. In this area, the jugal has an anterior process whose external surface is relatively straight and shallow, penetrated by a series of small foramina below the orbit. Its anterior margin is markedly indented to accommodate the two posterior projections of the maxilla and the lacrymal. A narrow, curved rod extends dorsally forming the posteroventral orbital rim, and passes behind the postorbital process. The rod thus contributes the bulk of the anterior rim of the infratemporal fenestra. A second, flattened but broader and thinner process extends dorsally as the posterior margin to this fenestra. A broad, flat, thin plate extends posteroventrally toward the quadrate, overlying the quadratojugal. Externally, the jugal is gently convex longitudinally and transversely.

SQUAMOSAL. Very little of the squamosal is preserved; all that remains is the posteroventral area. This extends mesially in contact with the parietal and is supported laterally by the paroccipital process.

QUADRATOJUGAL. This is a relatively thin, small, sheet-like plate positioned between the jugal and the quadrate. Posterodorsally, the quadrate appears to overlie the quadratojugal but ventrally, the quadrate is partially overlapped. A relatively large fenestra is present at the junction of the quadrate and quadratojugal. The bone does not extend ventrally as far as the jugal. It is broadly convex longitudinally and transversely, with a spine (now broken) at its ventral extremity.

Due to the relatively great anteroposterior length of the quadratojugal, the posterior bar of the infratemporal fenestra presents an unusually broad appearance in lateral view.

QUADRATE. The quadrate is a large, robust bone forming the posteroventral corner of the skull and bearing the articulating condyle for the lower jaw. The condyle is rounded anteroposteriorly and very gently convex transversely. It is expanded to a greater extent than the body of the bone immediately dorsal to it, this expansion being conspicuously greater mesially. The anterior surface above the condyle is gently concave transversely and longitudinally, whereas the posterior surface is strongly convex transversely and concave longitudinally. Sharp angles are produced where the surfaces meet anteromesially and anterolaterally. Above the condyle, the bone twists slightly. Dorsally, the quadrate is expanded anteriorly and probably contributes to the posterior wall the infratemporal channel. It is channelled anteriorly, near the quadratojugal by a fenestra to which it contributes the posterior, dorsal and ventral margins. In section, the dorsal part of the bone was broadly U-shaped, with the arms extending mesially.

A peculiarity of the quadrate is its orientation. The ventral articular end of the quadrate is located posterior to the dorsal portion of this element, so that the posterior surface slopes down and back. Although the dorsal extremity of the quadrate is not preserved, the position of the paroccipital process indicates that it was not placed posterior, or even directly above, the ventral articular end.

DENTARY. The dentary is incomplete anteriorly and ventrally. Below the middle of the tooth row, the mesial and lateral parts of the dentary are approximately parallel but posteriorly, they diverge considerably.

Laterally, the dentary, as preserved, is longitudinally concave. Although lacking, it is likely the anterior portion was longitudinally convex laterally. Inner surfaces of the dentary are correspondingly convex posteriorly and presumably concave anteriorly, probably giving the lower jaw a gently sinusoidal aspect in ventral view. The greater posterior thickness of the jaw is achieved external to the tooth row. Transversely, the lateral surface is gently convex anteriorly and strongly convex posteriorly, but the mesial surface has much less convexity.

The lower limits and external expression of the Meckelian canal are not preserved, although a portion of the splenial margin is present. Massive expansion of the canal occurs anterior and ventral to the coronoid process into an adductor fossa which increases in depth and width posteriorly. Several foramina occur along the lateral surface of the dentary, presumably for nerves and blood supply to the cheeks. The dentary is overlapped by the splenial but the relationship with the coronoid is unknown on the mesial surface. Laterally, the dentary overlaps the surangular and is overlapped by the coronoid.

SPLENIAL. The splenial is a very thin bone applied mesially to the ramus and is gently concave longitudinally and convex transversely. Its ventral extent is unknown.

ANGULAR. Only fragments of the angular remain. These suggest a relatively thin bone which tapers posteriorly where it overlaps a considerable portion of the surangular.

SURANGULAR. This is a relatively large bone, the extreme dorsal and the mesial aspects of which are still masked by matrix. It is laterally thin but much thicker posteroventrally. Longitudinally, the lateral surface is gently convex, except in the area immediately anterolateral to the articulation where a very strongly defined, and dorsolaterally projecting, rounded boss is present. Ventrally, it is gently longitudinally concave. A very large foramen is present anteriorly near the coronoid junction. Dorsally the surangular butts against the coronoid.

PREARTICULAR. This is visible ventrally and posteromesially. It is a flattened, thin bone which tapers posteriorly and thins anteriorly. Posteriorly, it becomes transversely convex and overlaps the articular.

ARTICULAR. The articular is somewhat masked by the quadrate, but appears triangular in dorsal aspect with the base anterior. The vertex is formed by a high, triangular dorsomesial expansion thickened posteriorly, that forms the retroarticular process. Anterior to this is the concavity for the quadrate articulation. The articular is overlapped laterally and ventrally by the bones anterior to it.

CORONOID. Still masked dorsally by matrix, the coronoid is a large element present as a dorsal extension of the ramus under the jugal. Its internal extent is unknown.

TEETH

Only maxillary teeth are exposed; the dentary teeth are present but are deeply masked by matrix. Anterior maxillary teeth are much smaller than those in the middle of the series and size of posterior teeth appears reduced compared with those in the mid-cheek area. The maxillary teeth are arranged in a single row.

MAXILLARY TEETH (Plate 2). The crowns of the teeth are laterally compressed and are wider than the roots whose extent and shape are unknown. The lateral surfaces of the crowns (and apparently the mesial side of dentary crowns) are covered by thin enamel. This is finely and evenly ornamented with vertical ridges and grooves with up to 13 ridges visible in teeth in the midmaxillary area. Considerable variation in numbers of ridges is evident however and anterior maxillary teeth have only 7 ridges. In unworn maxillary teeth, the secant occlusal surface is nearly straight but is angled obliquely posteriorly, with serrations corresponding with the position of the vertical ridges at the distal edge.

Wear with the dentary teeth maintains a sharp, enamelled lateral margin to the maxillary teeth and the tooth row rapidly assumes a straight, continuous cutting edge along the length of the skull. Mesially, the occlusal surface of the crowns assumes an inclined, concave wear facet.

The teeth curve slightly mesially. Posterolaterally, the crown is deeply, vertically grooved and it appears that this groove, like the lateral surface, is enamelled. Crowns are closely pressed together along their anterior and posterior margins. Mesially, each tooth slopes obliquely from the occlusal surface and near the socket, the crowns are very wide, the transverse dimension being even greater than the length of the crown. Fracturing of the skull reveals that replacement appears to have been alternate.

THE VERTEBRAL COLUMN AND RIBS

Because of disassociation it is unclear whether the vertebrae represented comprise the total number present during life. It appears likely that most presacral centra are present but judging from comparison with related forms, some posterior dorsal vertebrae are probably lacking. Remains of sacral vertebrae are present but shedding has been extensive in this region and insufficient exists for description. Caudal vertebrae are known from only a small series, presumably from the area immediately posterior to the sacrum. Distal caudal vertebrae are unrepresented and were probably lost before preservation.

The presacral series comprises 9 cervicals and a minimum of 15 dorsals. From attachment scars on the ilium, the number of sacral vertebrae appears to have been six. Neural arches throughout are poorly preserved.

ATLAS. This consists of an intercentrum, an odontoid process and two neural arches and is illustrated in Fig. 3. Largest of these components is the intercentrum, a subcrescentic bone with a large, shallow, anterior depression for the occipital condyle. Obliquely inclined, this depression has a sharply rounded edge ventrally. Two surfaces are

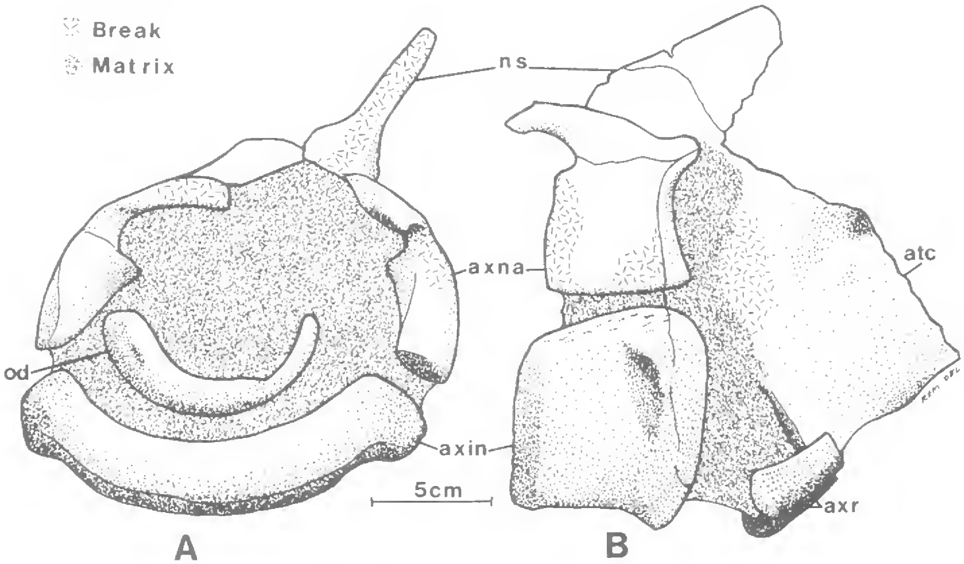

FIG. 3. Atlas-axis complex of *Muttaburrasaurus langdoni* (QM F6140) as preserved. A, anterior view; B, lateral view. Abbrev.: atc, atlantal centrum; axin, axial intercentrum; axna, axial neural arch; axr, axial ribs; ns, neural spine; od, odontoid process. The axial ribs and atlantal centrum are broken posteriorly, and have been rotated backwards and clockwise relative to the axis.

present laterally, directed dorsolaterally and slightly anteriorly for the neural arches. Ventrally, the surface is near planar anteroposteriorly, medially abruptly curving ventrally at the posterior margin, forming a distinct edge with the posterior surface. Posteriorly, the surface mesial to the rib facet is gently concave transversely and strongly convex dorsoventrally. The rib facet is broadly rounded.

The odontoid process is near planar anteriorly. The anterior crescentic area is flattened and slightly inclined, with a slight median depression for the occipital condyle.

The neural arches are irregular bones, separated from one another dorsally. Two articulating surfaces are present ventrally. The larger, directed anteroposteriorly and curving posteromedially is for the intercentrum, while the other faces anteromedially and forms a continuation of the intercentral articulation for the occipital condyle. Externally, the neural arches are broadly convex dorsoventrally, although a short, stout process is directed posterolaterally. Anteriorly, the area of the prezygopophysis is thin and flared, with two lobes, the inner of which is the more robust. The postzygopophysis is weakly defined, directed posteromedially. A strong concavity is present between this and the short posterolateral process.

The atlantal rib is small, laterally flattened and ovate in section. The head is slightly expanded with an obliquely inclined concave surface for articulation, broadly convex in lateral view.

AXIS. The axis is incomplete, being known only from the anterior moiety. The centrum is near planar anteriorly except for a shallow medial depression at the ventral margin. If an intercentrum was present, it must have been extremely small. The neural arch is well developed with a strong, laterally compressed neural spine, incomplete posteriorly. Anteriorly, the spine is slightly thickened. Prezygopophyses are transversely convex and the atlantal postzygopophyses articulated around their lateral surfaces. The suture between neural arch and centrum is indistinct.

A small fragment of the rib of the axis tapers rapidly posteriorly, suggesting it was very short. It is subtriangular to subovate in section and was probably single headed.

CERVICAL VERTEBRAE 3 TO 9 AND RIBS. All cervical vertebrae have opisthocoelous centra, although by cervical 9, the degree of concavity and convexity of the centrum has been considerably reduced. All have articulating ends that are broader than they are deep. The centrum of cervical 3 is ventrolaterally compressed resulting in production of a ventral crest which is broader posteriorly than anteriorly. The other cervical centra all have a well developed ventral keel.

The neuro-central suture is clearly above the parapophysis in all cervicals back to cervical vertebrae 8 and 9 where it straddles the suture. The parapophysis is comparatively small in cervical 3 but in posterior cervicals, it is considerably expanded. Diapophyses are poorly exposed and in most vertebrae have been lost along with the bulk of the neural arches. However in mid-cervical vertebrae they are robust, extending well out from the arch. Anterior cervicals have the parapophysis extended laterally and directed dorsolaterally. A broad ridge is developed laterally on all centra by dorsolateral compression of the centrum, giving the centrum a cruciate cross-section.

Prezygapophyses and postzygapophyses are robust and, in mid-cervical vertebrae, extend anteriorly and posteriorly to positions about one-third the length of the centra on either side. In cervical 6, a strong ridge is present running from the middle of the dorsomesial surface of the postzygopophysis towards the neural spine. This becomes weaker in more anterior vertebrae and is virtually lacking by cervical 5. A weak neural spine is present on cervical 5, becoming slightly stronger posteriorly. In anterior cervicals, the prezygopophysis appears continuous laterally with the margin of the centrum, but in posterior cervicals, the zygopophyses are separated from the central margins by excavated areas.

Cervical ribs are well preserved but are known only from the mid-cervical area. Heads are bifid, widely separated by a deep, lateral excavation which continues obliquely posterodorsally, and supported below by a continuation of the lateral ridge from the capitulum. The tuberculum is more robust than the capitulum and has a concave articulation. The rib of cervical 5 extends posteriorly to above the middle of cervical 7. The body of the rib is subtriangular in section, with the apex directed mesially.

DORSAL VERTEBRAE AND RIBS (Fig. 4). All centra of dorsal vertebrae are amphiplatyan to mildly amphicoelous. It is likely that the series preserved is incomplete and exact determination after dorsal vertebra 9 is uncertain. Length of the centrum remains reasonably constant back to the mid-dorsal region where a slight decrease in length is seen. More posteriorly, centra appear to be increasing in length. Width of dorsal vertebrae decreases from dorsal 1 to 6 then increases until width again exceeds length (Table 1).

In the first dorsal vertebra the centrum is laterally compressed, producing a ventral keel which is thicker and deeper anteriorly than posteriorly. The degree of compression decreases posteriorly so that the ventral part becomes progressively rounded.

The neural arches are poorly preserved although some anterior and mid-dorsal representation is present. The level of the diapophysis drops sharply from dorsal 1 to 3. Succeeding dorsals maintain the diapophyses at about the level of that on dorsal 3, at least to the mid-dorsal region. Anterior dorsal vertebrae have large prezygopophyses set widely apart but mid-dorsal examples are smaller and closer together. The articular surfaces of the prezygopophyses preserved are all inclined from the horizontal at a low angle of about 30°.

The angle between the transverse process and the vertical gradually widens posteriorly, from about 60° in dorsal 2 to about 75° in the mid-dorsal region. The first neural spines are thin, but they become thicker posteriorly. The posterior edge is much wider than the anterior. Spines appear to increase in height posteriorly but are not excessively developed.

Dorsal ribs are known only from sections, some

TABLE 1

VERTEBRAL MEASUREMENTS (CM)

Vertebra	*Length*	*Maximum Central Breadth*
Cervical 3	12·2	12·9
Cervical 5	13·6	13·2*
Cervical 6	12·2	12·8*
Cervical 7	11·6	14·9
Cervical 8	10·4	15·8
Dorsal 1	9·0	15·5
Dorsal a (anterior)	11·0	—
Dorsal b (anterior)	12·1	12·9
Dorsal c (mid)	11·3	11·3
Dorsal d (mid)	11·9	—
Dorsal e (posterior)	10·0	14·0
Caudal a	8·5	11·0
Caudal b	7·8	10·8
Caudal c	10·2	—

Exact position of lettered vertebrae not determined, sequence indicated by the sequence of lettering. Dorsal b follows dorsal a directly, as does dorsal d, dorsal c.

*Breadth estimated by doubling distance from midline to edge of centrum.

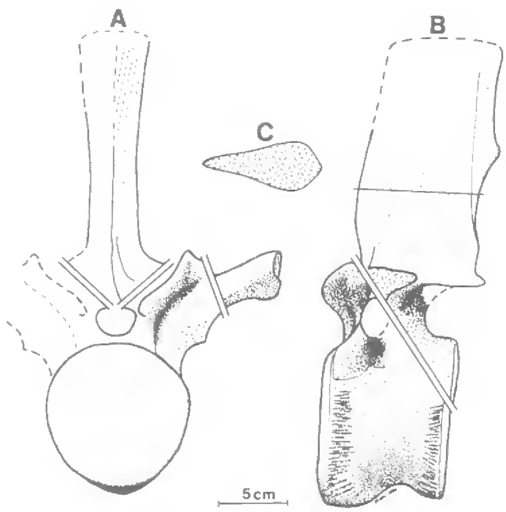

FIG. 4. Composite of two dorsal vertebrae of *Muttaburrasaurus langdoni* (QM F6140). Centrum and prezygapophysis of an anterior dorsal combined with arch and spine of a posterior dorsal. Unprepared posterior dorsals indicate that the central form is very similar between the anterior and posterior dorsals, but that the prezygapophyses are more nearly horizontal in the posterior dorsals. A, anterior view; B, lateral view; C, cross-section through spine at horizontal plane indicated in B.

preserved in correct position. Anterior and mid-dorsal ribs are double-headed and all are strongly curved close to their articulation. Distally, they are anteroposteriorly expanded and are flatter mesially than laterally, and this is still evident by dorsal vertebra 9. The capitulum is borne on the proximal end of the rib, while the tuberculum is on a more dorsolaterally placed step and faces dorsomesially. Anterior ribs have the capitulum and tuberculum widely separated.

SACRAL VERTEBRAE. Because of shedding, little can be said about sacral vertebrae other than that at least part of the series was fused. From interpretation of articulations on the ilium, it appears that 6 sacral vertebrae were present.

The single sacral (or dorso-sacral) centrum that has been completely freed from the matrix is deeply constricted, with amphiplatyan central articular surfaces. The (presumably) anterior articular surface has deep, radial grooves peripherally, some extending as much as two-thirds of the distance to the centre, but most rather shorter. The posterior surface bears irregular depressions, but nothing comparable to the grooves. The floor of the neural canal is deeply excavated, but is not yet entirely cleared so that the total depth of the excavation is not known. At the base of the pedicles, anteriorly, on each side there opens a large, U-shaped foramen running posteroventrally into the centrum.

CAUDAL VERTEBRAE. Very weathered caudal vertebrae are present and have been determined as being from the area immediately posterior to the sacrum. None have preserved a neural arch and all have suffered some degree of shedding. Measurements, mostly estimated, are listed in Table 1. Centra appear to be amphicoelous or amphiplatyan and become lower and thinner progressively back along the series. All have a somewhat squared appearance with lateral surfaces merging with ventral around sharply rounded ventrolateral borders Mid-ventrally, there is a deep pit in anterior caudals which is not due to crushing. The ventral margin slopes abruptly posteriorly in this area and a somewhat sharper slope defines the articulation for large chevrons, none of which has been preserved.

OSSIFIED TENDONS. Ossified tendons are present in the collection but preparation has not revealed any *in situ*. They appear to have been up to 0·5 cm in diameter.

THE PECTORAL GIRDLE

SCAPULA. Scapulae are preserved on both sides

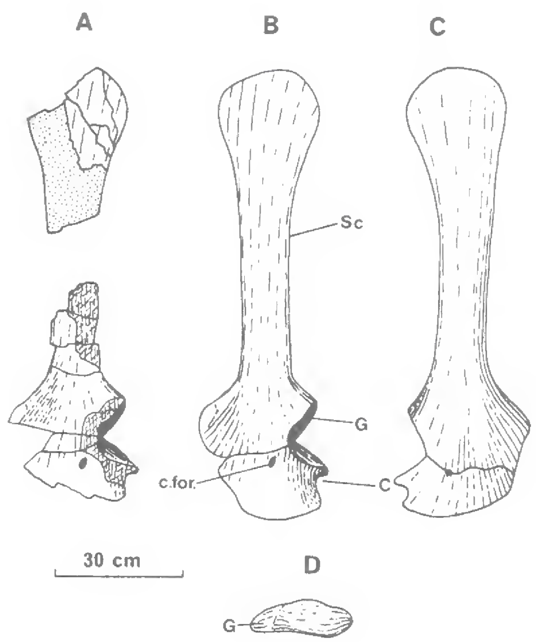

FIG. 5. Left scapulocoracoid of *Muttaburrasaurus langdoni* (QM F6140). A, lateral view as preserved; B, lateral view reconstructed; C, medial view reconstructed; D, glenoid aspect reconstructed. Abbrev.: C, coracoid; c.for., coracoid foramen; G, glenoid; Sc, scapula. Hatched areas represent broken surfaces.

but that on the right is better represented. Contact between the proximal and distal extremities is not preserved. The scapula is illustrated in Fig. 5.

The bone is apparently long and slender but is much more robust proximally. The distal end is expanded and the shaft is gently curved, conforming with the shape of the rib cage. From the mid-shaft area the dorsal border is nearly straight, but ascends abruptly anteriorly at the coracoid contact. A well-defined facet is present for the coracoid. Externally, the proximal end is broadly convex but internally the surface is concave. Ventrally, it is expanded into a posteroventral extension, comprising the bulk of the glenoid cavity. Both the glenoid cavity and the articulation for the coracoid are rugose. The anterior edge of the scapular blade is thin and rounded as is the posterior edge, continuing slightly onto the dorsal surface. The dorsal edge is thicker.

CORACOID. Coracoids are known from fragments from both sides and the element is figured in Fig. 5. The bone is apparently small, short and deep. It is thick along the scapular facet, while the distal portion become much thinner. Externally the bone is shallowly concave over the dorsal two-thirds and convex towards the ventral border. It is broadly sigmoid internally and externally along the scapular articulation and the coracoid contributes slightly less to the glenoid cavity than does the scapula. The articulation is sigmoid, ovate and rugose. The coracoid foramen is complete and opens internally in a broad notch along the articular margin. Ventrally, the margin is sharply concave anterior to the glenoid cavity limit.

STERNUM

Sternal bones have not been located with certainty, although fragments may represent these elements.

THE FORE-LIMB

HUMERUS. The humerus is incompletely represented from the left side. As with other limb bones, shedding and bone loss have occurred particularly in the mid-shaft region and have proceeded to the extent of excluding contact between proximal and distal parts. This is shown in Fig. 6, while measurements are listed in Table 2.

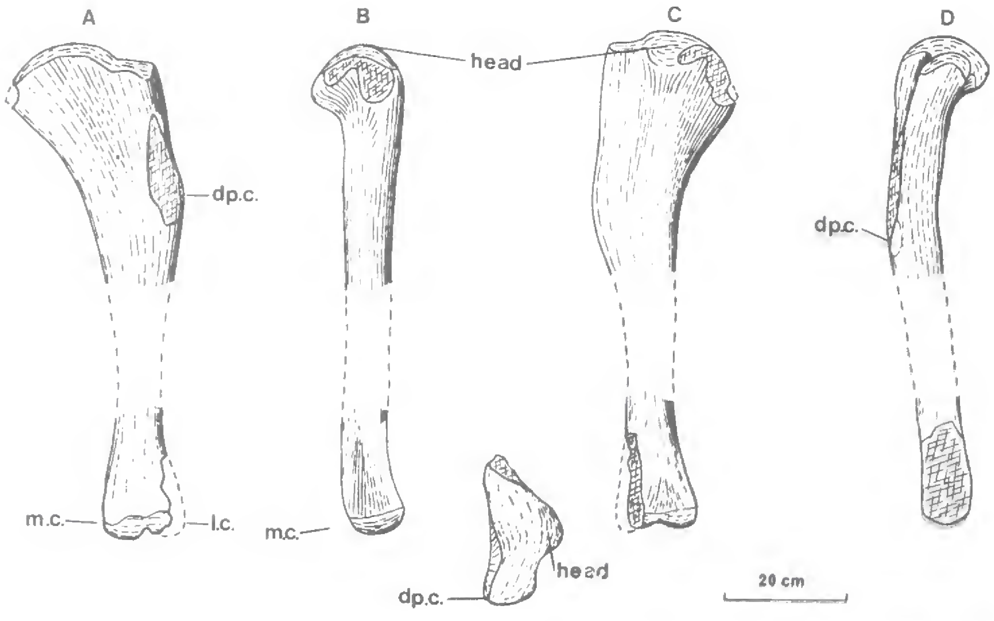

FIG. 6. Left humerus of *Muttaburrasaurus langdoni* (QM F6140). A, anterior view; B, medial view; C, posterior view; D, lateral view; E, proximal view. Abbrev.: dp.c., deltopectoral crest; l.c., lateral condyle; m.c., medial condyle. Hatched areas represent broken surfaces.

TABLE 2

MEASUREMENTS OF GIRDLE AND LONG BONES (CM)

Element	*Length*	*Proximal width*	*Distal width*
Scapula, lt.	—	27·7*	—
Coracoid, lt.	—	26·1*	—
Radius, lt.	—	10·5	8·7
Ulna, lt.	—	14·4	10·2
Femur, rt.	101·5	34·4	34·0
Tibia, rt.**	96·2	—	—
Fibula, rt.	—	19·7	11·6

*at glenoid border
**with calcaneum + astragalus

The humerus is elongate being the longest element of the fore-limb. It exhibits a sigmoidal flexure in lateral view, the proximal end being more posteriorly positioned than the distal end. Proximally, the head is expanded transversely and posteriorly. Towards the centre of the shaft, the posterior surface is broadly convex whereas the anterior surface is nearly flat, these being joined by rounded margins. The medullary cavity is extensive, at least in the mid-shaft region. The proximal moiety of the bone is strongly curved medially, with the head positioned internal to the plane of the distal moiety. The head is subspherical, positioned approximately in the centre of the proximal surface, supported by a strong buttress arising abruptly from the posterior surface of the shaft. Greater and lesser tuberosities are well developed. The proximal surface, particularly of the head, is rugose. Below the head, the anterior surface is broadly concave, particularly towards the weakly-developed deltopectoral crest which extends well down the length of the shaft. The crest progressively thickens distally toward the apex and its margin is rounded.

Distally, the humerus is robust and heavy, being more expanded transversely than anteroposteriorly. Both the radial and mesial condyles are defined and are separated by a deep, wide concavity for the olecranal process. The mesial condyle is produced more distally than the radial condyle but the latter slopes anterolaterally from the posterior surface while the former has a mesial surface which is rounded but near vertical. The posterior surface of the distal end is slightly concave and the articulation is rugose. The supinator ridge is moderately well developed.

ULNA. Only the left ulna is preserved and a mid-shaft fracture has minimal contact. Measurements are provided in Table 2 while the bone is illustrated in Fig. 7. The ulna is somewhat longer and considerably heavier than the radius but is shorter than the humerus. It is more expanded proximally than distally. Part of the olecranal process is lacking but the process was apparently not extensive. The articulating surface is shallowly concave and moderately narrow. Anteriorly, the surface of the shaft and the head are shallowly concave to accommodate the radius, while mesially the shaft is flattened.

The ulna is slightly expanded distally and shows moderate anterior concavity. Posteriorly, the bone is correspondingly convex. The long axis of the distal expansion is inclined to that of the proximal expansion at an angle of 60°. the articulating surface is rugose and is broadly convex in both directions. Towards the centre, the shaft narrows and is subtriangular in section with a small medullary cavity.

RADIUS. Only the left radius is preserved and, although nearly complete, has minimal contact in the mid-shaft area. Its measurements are presented in Table 2 and it is shown in Fig. 7. It is the smallest and shortest bone of the fore-arm. Its distal end is somewhat expanded with an approximately semicircular articulation. The shaft is not greatly constricted. In section, it is subelliptical towards the mid-shaft region with the long axis directed anteroposteriorly, the section becoming more circular proximally.

The articulation of the elbow was located *in situ*.

CARPALS. The bones of the wrist are preserved

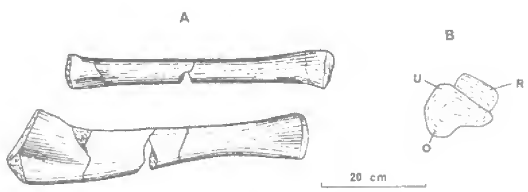

FIG. 7. Antebrachial elements of *Muttaburrasaurus langdoni* (QM F6140). A, lateral view; B, proximal view. Abbrev.: o. olecranon; R, radius; U, ulna. Hatched areas represent broken surfaces.

only on the left side. Because of partial disassociation they are difficult to interpret and it is uncertain whether all elements present have been preserved. Six elements only are discernable.

Only a fragment of the radiale is preserved, this closely adpressed to the lateral margin of the intermedium.

The intermedium viewed anteriorly (and allowing for slight loss posterodorsally) was semi-circular in shape with a truncated anterodorsal corner. Remains of a large distal carpal element exist below the intermedium.

The ulnare is cushion-shaped with a smooth, concave proximal surface forming the chief contact with the ulna. The posterior surface is concave. It appears to slightly over-ride the margin of the intermedium, with which it articulates. Remains of a small carpal element, possibly C5, are present lateral to the ulnare.

A further large distal carpal element is present below the ulnare. All carpals are well ossified with clear articular relationships.

METACARPALS. Only two metacarpals from the left forefoot are known and these have been interpreted as metacarpals IV and V. Measurements are listed in Table 3.

Metacarpal IV is short and stout and is constricted mesially, with moderately expanded articular ends. The proximal articulation is slightly concave transversely and slightly convex dorsoventrally. Distally, the articulation is more strongly convex. In section, the shaft is subcircular.

TABLE 3
MEASUREMENTS OF MANUAL AND PEDAL ELEMENTS (CM)

Element	*Length*	*Proximal width*	*Distal width*
Metacarpal IV	8·7	5·6	5·1
Metacarpal V	7·7	—	5·3
Phalanx IV, 1	4·4	4·6	—
Phalanx IV, 2	2·6	4·0	—
Phalanx V, 1	4·0	4·7	—
Phalanx V, 2	2·9	3·6	—
Phalanx V, 3	2·2	2·2	—
Metatarsal I	—	7·7	—
Metatarsal II	45·9	11·2	11·8
Metatarsal III	—	10·9	14·0
Phalanx II, 1	11·1	12·7	—
Phalanx II, 2	10·5	9·8	—
Phalanx III, 1	—	14·4	—
Phalanx III, 2	11·7	12·8	—
Phalanx IV, 1	16·1	11·5	—

Metacarpal V is similar in shape to metacarpal IV but is slightly shorter and slightly less robust.

PHALANGES. Again, well preserved phalanges are only known from the left manus, associated with the metacarpals interpreted as IV and V and are illustrated in Plate 2 with measurements listed in Table 3. Digit IV has at least three phalanges present while digit V has four. Additional fragmentary, isolated phalanges are present but cannot be assigned with certainty.

The proximal phalanx of digit IV is robust and short. The dorsal rim of the proximal articulation is weakly convex whereas the articulation is dorsoventrally weakly concave. The mesial extension of the distal articulation is produced to a greater extent than the lateral. The dorsal rim is deeply concave while the articulation is dorsoventrally convex. Ventrally, the bone is somewhat flattened while it is somewhat convex dorsally. The second phalanx is considerably smaller. Dorsally, it is weakly convex proximally and concave distally. Only part of the proximal articulation of the third phalanx of digit IV is preserved.

The proximal phalanx of digit V is slightly shorter than that of digit IV and appears to have been less robust. The second phalanx is slightly longer than its counterpart in digit IV. The third phalanx is short and reduces in width rapidly towards its distal end. A very small, sub-circular nugget of bone is preserved as a continuation of this digit which is interpreted as the terminal phalanx of digit V.

An isolated fragmentary element, interpreted as the ungual phalanx possibly from digit II, is very large, robust and tapers anteriorly.

An incomplete element from which there has been much shedding, seems to represent a manual spike comparable to that of *Iguanodon*. The flattened element tapers strongly from a slightly convex basal articular surface, apparently toward an apex now missing. If this is properly interpreted as a manual spike, it was larger with respect to the metacarpals than in *Iguanodon*.

THE PELVIC GIRDLE

ILIUM. The right ilium is almost complete but only weathered fragments of the left are preserved. Although incomplete, the anterior process accounts for about two-fifths of the total ilial length (Fig. 8). Measurements for the ilium appear in Table 2. The shallow process is directed ventrally and laterally apparently to clear the ribs. The dorsal surface is inflated medially from above the centre of the acetabulum, anteriorly to near the limit of the anterior process and is reasonably strongly sinuate in outline from above and broadly convex laterally.

The bone is deepest and thickest above the anterior portion of the acetabulum. A slight lateral expansion of the dorsal border is present above the level of the anterior acetabulum extending anteriorly to above the level of the preacetabular notch. Generally, the ilium is thin. Dorsoventrally, the lateral surface is weakly concave from above the preacetabular notch anteriorly along the anterior process. Internally, the body of the ilium is more strongly concave, with the development of a strong, tuberculate ridge above the articular facets for the sacrum. This ridge exists along the bulk of the length of the ilium from above the base of the anterior and postacetabular processes, extending about midway between the dorsal margin and the acetabulum in the main body of the ilium. Articular facets for the sacral vertebrae are poorly defined but are present between the pre- and postacetabular notches.

The postacetabular process is slightly incomplete. It appears that the mesial shelf developed towards the base may disappear before reaching the posterior extremity. Length of the process from the ischial tuberosity is about one-quarter the ilial length as preserved. The preacetabular notch is moderately wide. The public peduncle is long and deflected. Within the acetabulum, the inner surface of the pubic peduncle is moderately expanded laterally and ventrally from above providing a moderately concave roof for the head of the femur. The acetabular broader is well defined anteriorly but less well defined posteriorly. The ischial peduncle swells rapidly posteriorly and laterally forming a strongly concave tuberosity for the articulation of the ischium. In its contribution to the acetabulum, it has a rugose articular surface. Anteriorly the medial margin of the ilial acetabulum is prolonged ventrally to partially wall the acetabulum medially. The postacetabular notch is virtually absent being represented only by a weak, broad concavity.

PUBIS. Parts of the pubis are known from both sides. The bone shown in Fig. 8 and measurements appear in Table 2. Although contact is poor, little of the prepubic process is believed missing. It is elongate and deep. The blade is thin and slightly

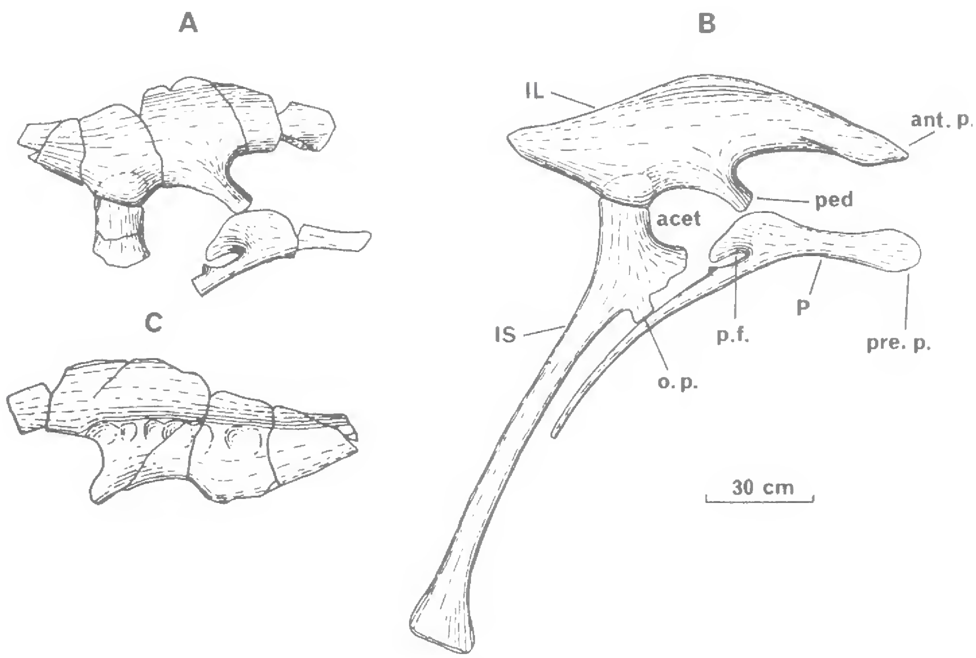

FIG. 8. Right pelvis of *Muttaburrasaurus langdoni* (QM F6140). A, lateral view of pelvic elements as preserved; B, lateral view of pelvis reconstructed; C, ilium in medial view. Pubis in A represents portions preserved of both right and left pubes. Abbrev.: acet, acetabulum; ant.p., anterior process; IL, ilium; IS, ischium; o.p., obturator process; P pubis; ped, pubic peduncle; p.f., pubic foramen; pre.p., prepubic process.

expanded distally, producing a marked dorsal concavity behind the anterior margin. The dorsal margin is thicker than the ventral which appears to be subacute. The process is slightly sigmoidal in dorsal view.

The main body of the pubis is thicker, especially dorsally. A subtriangular facet is present dorsally which articulates with the pubic peduncle of the ilium. The acetabular border is anteroposteriorly concave, moderately broad and shallowly concave transversely. Again the medial margin rises to form a medial wall for the acetabulum, especially anteriorly. The acetabular border is approximately ovate in shape, extending posteroventrally as a moderately extensive process. The process dorsally bounds a large pubic foramen. The postpubis borders the foramen ventrally and has a short projection of bone which incompletely encloses the foramen posteriorly. The postpubis is very slender but largely missing.

ISCHIUM. Each ischium is represented by the proximal ends only (Fig. 8). The proximal end has a broad, deeply curving proximal border forming a part of the ventral and posterior acetabular boundaries. The articular surface for the ilium is expanded laterally and is posteriorly convex and anteriorly concave transversely and slightly concave anteroposteriorly. The surface is rugose. The articulation is complete with the ischial peduncle of the ilium. Below the ilial branch, the ischium becomes narrow and plate-like. The pubic branch and the obturator process are lacking.

THE HINDLIMB

FEMUR. The femur is reasonably well known from both sides of the body but in each, shedding has occurred in the mid-shaft region. Fig. 9 illustrates the extent of this as well as a reconstruction.

The femur is the longest and most robust bone in the hindlimb. Measurements are provided in Table 2. The shaft is strongly curved in the parasagittal plane. The head is clearly defined, set nearly at right angles to the shaft. It is robust, sub-spherical with the dorsal surface rugose, and with the neck compressed anteroposteriorly. A shallow, well-defined groove extends on the posterior surface from the head towards the body of the shaft.

The greater trochanter is massive, widely expanded anteroposteriorly and gently convex proximally, produced to about the same level as the plane of the head. The dorsal surface between the head and the greater trochanter is shallowly concave. The lesser trochanter is a large structure originating from the anterolateral border of the shaft and produced proximally to about the same level as the great trochanter, separated from it by

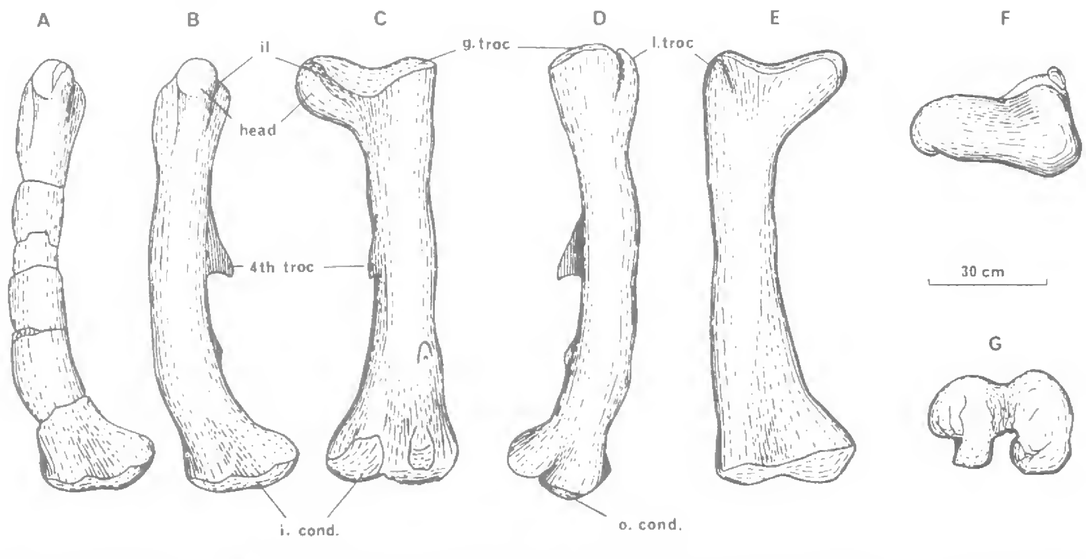

FIG. 9. Right femur of *Muttaburrasaurus langdoni* (QM F6140). A, F and G, femur as preserved, others reconstructed. A and B, medial view; C, posterior view; D, lateral view; E, anterior view; F, proximal view; G, distal view. Abbrev.: g.troc, greater trochanter; i.cond., medial condyle; il, fossa for ischial peduncle; l.troc., lesser trochanter; o.cond., lateral condyle; 4th troc, fourth trochanter.

a deep, narrow cleft. It is placed anterolateral to the greater trochanter. The anterolateral border of the shaft is subangular in the proximal one-third owing to a ridge from the lesser trochanter base which continues to curve across the anterior face of the shaft. This divides two flattened surfaces almost at right angles to one another. Posteriorly the shaft is longitudinally concave. The base of a large fourth trochanter is present posteromesially. An isolated fourth trochanter shows this structure to have been pendant in its free extent.

Distally, the shaft terminates in well-developed inner and outer condyles, separated by a deep, intercondylar groove. The inner condyle is more robust than the outer and its articular surface is more extensive. The interior, dorsal border of the inner condyle shows coarse striations. The intercondylar groove has a deep, narrow extension into the body of the inner condyle, approximately opposite a shallow concavity on the mesial surface. A deep cleft bounds the outer condyle posterolaterally. Strong ridges ascend the body of the shaft posteriorly from the inner and outer condyles giving the shaft a concave popliteal surface. The lateral ridge is expanded at a position about one-third the length of the femur from the distal end into a lateral supracondylar tuberosity with a shallow pit directed posteriorly. Distally the anterior surface of the shaft is broadly concave longitudinally to form a shallow anterior intercondylar sulcus then markedly swollen opposite the lateral supracondylar tuberosity. The distal articulating surface is extremely rugose.

TIBIA. Tibiae are preserved on both sides but the right is more complete. In each, shedding has occurred in the mid-shaft region. The right tibia is illustrated in Fig. 10 together with a reconstruction. The bone is robust and slightly shorter than the femur. Its proximal extremity is heavier than the distal and is expanded both laterally and anteroposteriorly, the latter expansion being the greater. This expansion occurs on the mesial portion of the head and produces a robust inner condyle, separated by a deep, narrow popliteal notch from a strong outer condyle. The proximal articular surface is rugose and convex with the inner condyle contributing considerably more than the outer to its area, but both extend posteriorly to about the same extent. Anterolaterally, a broad cnemial crest is present which extends somewhat diagonally well down the length of the shaft.

Posterior to the crest is a gently concave surface for the inner surface of the fibula. The anteromesial margin of the shaft in this area is broadly convex transversely. The extension of the cnemial crest passes internally to merge with the base of the inner malleolus. Towards the middle of the body of the shaft, expansion occurs laterally

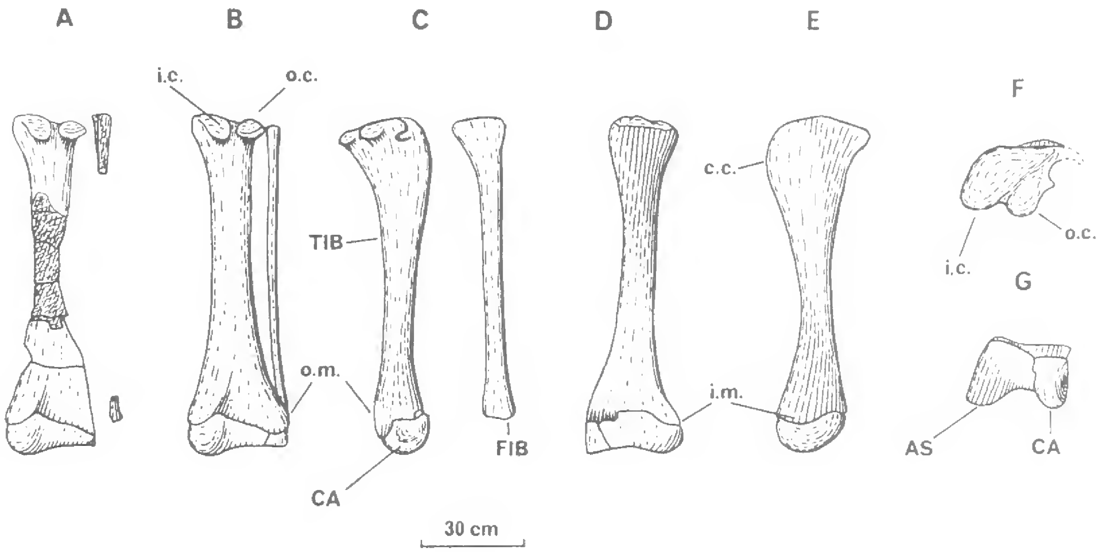

FIG. 10. Right crus and proximal tarsus of *Muttaburrasaurus langdoni* (QM F6140). A, F, and G, materal as preserved, others reconstructed. A and B, posterior view; C, lateral view; D, anterior view; E, medial view; F, proximal view; G, distal view. Abbrev.: AS, astragalus; CA, calcaneum; c.c., tibial crest; FIB, fibula; i.c., medial condyle; i.m., medial malleolus; o.c., lateral condyle; o.m., lateral malleolus; TIB, Tibia.

with resultant rotation of the greatest breadth of the bone, this continuing to the distal end. The anterior surface distally is nearly flat, with a shallow anterolateral depression for the distal end of the fibula. The concavity between the distal malleoli continues for only a short distance along the shaft. The articulation for the astragalus and calcaneum is broadly and deeply concave transversely and convex anteroposteriorly. A strong ridge ascends from the highest point along the posterior border.

FIBULA. The proximal portions of both fibulae and the distal extremity of the right fibula are represented. The extent of the bone preserved is indicated, reversed, in Fig. 10, together with a reconstruction. The bone was long and slender, and measurements appear in Table 2. On the right side the distal portion of the tibia retains its articulation with the astragalus and calcaneum, and the distal portion of the fibula may also be articulated here. The position of the latter shows that the fibula must have been slightly shorter than the tibia.

The proximal end of the fibula is expanded anteroposteriorly, the posterior expansion being the greater, with a broadly convex outer margin and a shallowly concave inner margin closely juxtaposed with the head of the tibia. The proximal articular surface is gently convex transversely and rugose. The anteroposterior breadth of the bone continues greater than the transverse below the head, but towards the middle of its length the shaft becomes subtriangular in section.

Distally, the extremity is incomplete but robust. Anterolaterally it is produced into a low, rounded process. A medial break and the position of the astragalar articular surface for the fibula indicate that it must have curved anteriorly around the tibia to articulate mesially with a dorsolaterally placed surface of the astragalus.

ASTRAGALUS. The astragalus is the largest bone of the tarsus. It has been preserved on both sides, fused with the calcaneum and closely adhering to the tibia. It is illustrated in Fig. 10 showing its greater mesial than lateral depth. Distally, the articulation is strongly convex anteroposteriorly and concave transversely. A low broad process is present at the posterior proximal border opposite a strong ridge on the tibia. Anteriorly, a low ascending process forms a junction with the tibia, is broadly convex transversely but laterally a strong, but low process is present bearing the dorsolaterally facing articulation for the fibula (Fig. 11).

The distal articulating surface is coarsely rugose. The proximal articulation is concave anteroposteriorly. When in articulation, the astragalus is much more exposed anteriorly than posteriorly.

CALCANEUM. Both calcanea are preserved but that on the left side is more complete. The bone is illustrated in Fig. 10 and is closely associated with the tibia and fused with the astragalus. Anteriorly,

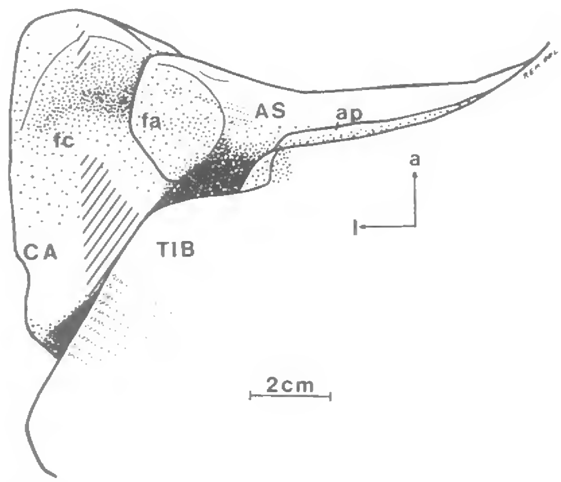

FIG. 11. Dorsal view of left proximal tarsus in articulation with tibia, of *Muttaburrasaurus langdoni* (QM F6140) showing the fibular facet of the astragalus. Abbrev.: a, anterior; ap, ascending process of the astragalus; AS, astragalus; CA, calcaneum; fa, fibular facet of astragalus; fc, fibular facet of calcaneum; l, lateral; TIB, anterior face of tibia. Diagonal lines represent broken surfaces.

the border of the calcaneum is approximately as deep as the posterior border. In anterior view, it is less exposed than the astragalus. The proximal surface is transversely and anteroposteriorly concave. The exposed articulation for the fibula is strongly concave anteroposteriorly and transversely is strongly concave to accommodate the posterolateral margin of the tibia, this being separated from the tibial articulation by a sharp, strong ridge. The distal articulation is rugose, broadly convex anteroposteriorly and weakly convex transversely.

DISTAL TARSAL I. Only a small fragment, possibly representing this element, has been located, closely adhering to distal tarsal II from the right side but it is too fragmentary to warrant description.

DISTAL TARSAL II. This element is known from both sides (Fig. 12). On the left side it is preserved somewhat displaced above metatarsal II and part of metatarsal III. It is a relatively thin bone, subhexagonal in proximal view and with an anteroposteriorly convex articulating surface. Transversely, this surface is slightly concave while the inner border is deeper than the outer. It articulates proximally with the astragalus. The distal articulating surface is slightly concave and is marked by a low, broad ridge running transversely from the lateral aspect towards the centre of the surface. Measurements are provided in Table 3.

METATARSALS. No metatarsal is preserved completely. Fragmentary remains are known from both sides but the left foot is more completely preserved. This is illustrated in Fig. 12 together with a reconstruction and measurements are provided in Table 3.

Proximal and distal ends of metatarsals II–IV are known for the left foot but all bones have been broken in the mid-shaft region. Only metatarsal IV has its length confirmed by fitted fragments but shape of the shaft in this and other metatarsals has been modified by shedding. Metatarsal IV appears to have been a long, relatively slender bone, the longest of the metatarsal series. Its proximal end, although incomplete, is rugose and is expanded both anteroposteriorly and transversely but the former is the greater. The articulation is nearly flat. In the shaft area, an anteromesial angle is present. Distally, the bone is slightly angled laterally. The head is expanded in both mesial and lateral moieties with the articulation rugose, transversely broad and deep, strongly convex anteroposteriorly and weakly concave transversely.

Metatarsal III is the heaviest element. Its proximal articulation is flattened and rugose but a narrow, deep notch is present about mid-way along its lateral rim. The head is slightly incomplete but is much more expanded anteroposteriorly than transversely. The transverse expansion is greater anteriorly and posteriorly than above the centre of the shaft, giving the head a waisted appearance in proximal view. Anteriorly, the head somewhat overhangs the shaft, this being more pronounced at the anterolateral border. The shaft is very angular anteromesially and considerably less angular anterolaterally. The

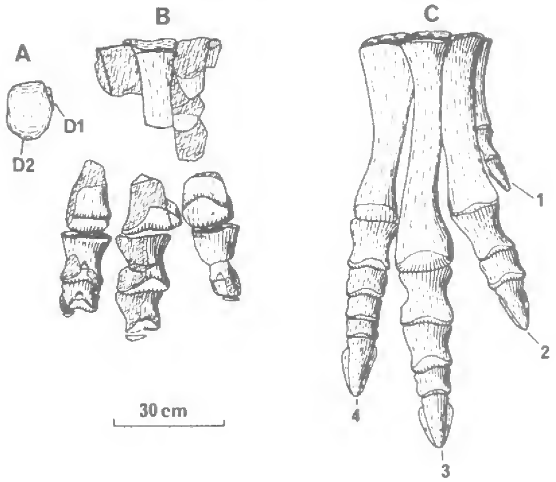

FIG. 12. Right pes of *Muttaburrasaurus langdoni* (QM F6140). A, the distal tarsals preserved; B, pes as preserved; C, pes reconstructed. Abbrev.: D1, distal tarsal 1; D2, distal tarsal 2.

anterior surface is flattened towards the proximal end. Distally, the bone is considerably expanded, this being greater transversely than anteroposteriorly. Deep depressions are present laterally and mesially. The articulation is rugose, broadly convex anteroposteriorly and shallowly concave transversely.

Metatarsal II is moderately robust. Its proximal articulation is partly masked by tarsal II but is rugose and apparently flat. It is expanded more strongly anteroposteriorly than transversely. The shaft appears more angular anterolaterally but shedding has occurred anteromesially. Distally, the bone is expanded but the anteroposterior expansion here remains greater than the transverse. The lateral portion of the distal articulation appears much stronger than the mesial, directing the articulation slightly inwards. The head is rugose, broadly convex anteroposteriorly and shallowly concave transversely.

There is no indication of metatarsal V, and if present it was excluded from the foot. The right metatarsus is less complete than the left, the distal ends of three metatarsals and the proximal ends of two being represented. One of these proximal ends however (*vide* Table 3) is considerably smaller than any of those of the left metatarsals, and of different form. It is thus interpreted as the proximal end of metatarsal I. The proximal articular surface is subtriangular in proximal aspect and strongly convex anteroposteriorly. It is slightly rugose. Little of the shaft is preserved but indicates that the cross-section was basically in the form of a thin isoceles triangle with the base directed anteriorly.

PHALANGES. Some phalanges from both feet are preserved but those from the left side are more complete. Extent of preservation is indicated in Fig. 12 and measurements are presented in Table 3. The reconstruction includes elements which are not represented at all. Only proximal elements of digits II–IV are known.

The proximal element of digit II is the longest in the foot. Its proximal articulation is considerably expanded and obliquely subovate, the outline being generally rounded except ventrally where a reasonable concavity is present. The articulation is slightly concave. The mesial surface of the shaft is convex while the lateral surface is flattened. Distally, the articulation is expanded. Deep depressions are present laterally and mesially, flanked by heavy, rounded ridges around the margins of the articular surface. No other phalanges are preserved on digit II.

The proximal phalanx of digit III is moderately elongate and is more robust than that of digit II. The proximal articular surface is similar to that in digit II but is slightly less concave ventrally and its oval outline is not oblique. The mesial moiety of the distal articulation is slightly more extensive than the lateral. Deep mesial and lateral depressions are present bounded by strong, rounded ridges limiting the articular surface. The second phalanx of digit III is short compared with the first (Table 3). Proximally, the dorsal and ventral borders are expanded into lips which fit around the articulation of the first phalanx. The lateral borders of the expanded proximal articulation are hollowed with the mesial moiety larger than the lateral. The distal articulation is concavoconvex to fit the third phalanx. Depressions are present mesially and laterally at the distal end of the shaft. Only the dorsal and ventral lips of the third phalanx are preserved.

In digit IV, the proximal phalanx is robust and short; shorter than those in digits II and III (Table 3). The articulating surface of the proximal end is concave and subovate, being flattened ventrally and more vertical mesially than laterally. Its distal articulation is approximately symmetrical like that in the corresponding bone of digit III, but the lateral moiety slopes outwards slightly more than the mesial. The lateral and mesial depressions are, however, less well defined. The second phalanx is relatively short (Table 3). It is like the corresponding bone of digit III, but is more vertical mesially than laterally. Lateral and mesial depressions near the distal articulation are comparatively shallow.

COMPARISON

INTRODUCTION

Recently much work has appeared on the non-hadrosaurian ornithopods. Galton has studied *Camptosaurus* (1980), *Dryosaurus* (1977a), *Hypsilophodon* (1974a), *Parksosaurus* (1973b), *Thescelosaurus* (1974b), *Valdosaurus* (1977b), *Vectisaurus* (1976) and the fabrosaurids (1978). He has not had the field to himself: Dodson (1980) is studying *Camptosaurus* and *Tenontosaurus*, Norman is working on *Iguanodon*, Rozhdestvenskii (1966) has described *Probactrosaurus*, Santa Luca (1980) has described *Heterodontosaurus*, Thulborn both fabrosaurs (1970a, 1970b, 1971, 1972, 1974) and hypsilophodontids (1973), and Taquet *Ouranosaurus* (1976). Hadrosaurs as well have had their share of work: Ostrom (1961), Rozhdestvenskii (1965, 1968) and Dodson (1975).

We can do no better than to quote Dodson (1980): 'Suddenly ornithopods have become a very-well studied group.'

Galton (1972) redefined the families of non-hadrosaurian ornithopods, later (1978) refining his definition of the Fabrosauridae. Basically Galton considered the Iguanodontidae as a grade of large, graviportal, non-hadrosaurian ornithopods (see also, Galton, 1974b). Dodson (1980) has pointed out the unsatisfactory nature of this definition and implicitly presented a new definition exemplified with *Camptosaurus*. Dodson's definition, restricted to the postcranial anatomy, comprised the following features:

(1) scapular blade constricted with strong flare at coracoid articulation;
(2) prominent acromion with clavicular facet;
(3) coracoid short with respect to scapular length;
(4) coracoid subquadrate in form, with abrupt craniodistal angle;
(5) coracoid foramen near the scapular articular surface, opening mesially at the scapulocoracoid articulation;
(6) humerus relatively short and narrow;
(7) deltopectoral crest weak, giving a proximal to distal taper to the humerus;
(8) radius distally compact and rounded;
(9) carpus compact and heavily ossified;
(10) carpal articular relationships well defined;
(11) three proximal and five distal carpals present;
(12) ilium massive, with straight dorsal margin;
(13) moderate medial reflection of postacetabular ventral margin of ilium;
(14) prepubis deep and flat, postpubis stout and decurved;
(15) ischial shaft rounded and decurved with distal expansion;
(16) femur curved with prominent lesser trochanter;
(17) well-defined anterior intercondylar sulcus on femur;
(18) pes short and stocky, metatarsus and digits broad.

This is almost a description of *Muttaburrasaurus*.

Galton (1977a) illustrates variations found in skeletal elements of *Hypsilophodon foxii*. Some of Dobson's criteria (e.g. constriction of the scapular blade, subquadrate form of coracoid) here seem to occur as individual variations. Such variation however is difficult of interpretation. Some modern tetrapods, *Trichosurus vulpecula* (brushtail possum) and *Trichosurus caninus* (bobuck) among mammals and *Amphibolurus nuchalis* and *Amphibolurus reticulatus* as well as *Ctenotis robustus* and *Ctenotis arcanus* (Czechura, pers. comm., 1980) among reptiles, would be virtually impossible to distinguish from skeletal material alone. Such osteological differences as exist would be interpreted as individual variations were these species known only from fossil material. Furthermore there is no suggestion that *Camptosaurus* exhibits the variation reported in *Hypsilophodon*, and thus we shall adopt here Dodson's (1980) criteria.

Comparison

The close agreement of *Muttaburrasaurus* with *Camptosaurus* in the features given by Dodson (basic agreement in fifteen of eighteen features, the remaining features being not determinable from the incomplete material of *Muttaburrasaurus*) implies that *Muttaburrasaurus* is an iguanodontid. Thus this section will include a brief comparison of *Muttaburrasaurus* with the other ornithopod families, but a more extensive comparison with the other well known iguanodontid genera.

In addition to being much larger and later than any known fabrosaurids, *M. langdoni* differs from the Fabrosauridae (Galton, 1978) in having: inset maxillary and dentary toothrows; a continuous, homodont dentition; well-defined occlusal wear surfaces on the maxillary dentition; ilium without lateral supra-acetabular flange; robust limb bones; and femur with massive greater trochanter. It differs from the Heterodontosauridae in lacking caniniform teeth and in having a well-developed anterior process to the pubis. (Galton, 1972). It differs from the Hypsilophodontidae in having a continuous wear facet on the maxillary teeth in one plane (Galton, 1972). It differs from the Hadrosauridae in lacking a dental battery of multiple tooth rows, but having only a single row each of maxillary and dentary teeth; having a reduced number of cervical vertebrae; and lacking a well-developed antitrochanter on the ilium (Lull & Wright, 1942).

Muttaburrasaurus langdoni shares the following characteristics with the iguanodontids, specifically with *Camptosaurus:*

(1) scapular blade constricted with strong flare at coracoid articulation;
(2) prominent acromion;
(3) coracoid short with respect to scapula;
(4) coracoid foramen near articular surface for scapula, opening mesially at the scapulocoracoid articulation;
(5) humerus relatively narrow;
(6) deltopectoral crest weak;
(7) radius distally compact and rounded;
(8) carpus compact and heavily ossified;
(9) carpal articular relationships well-defined;
(10) ilium massive;
(11) medial postacetabular ventral margin of ilium reflected;
(12) prepubis flat and deep;
(13) femur curved with prominent lesser trochanter;
(14) well-defined anterior intercondylar sulcus on femur;
(15) pes short and stocky, metatarsus and digits broad.

Muttaburrasaurus is clearly referrable to the Iguanodontidae on postcranial characteristics. *M. langdoni* shows some specific similarities to *Camptosaurus* which it does not share with the other well-known genera of iguanodontids (*Iguanodon, Ouranosaurus, Probactrosaurus,* and *Vectisaurus*). These include the possession of a skull that is low and broad, especially in the postorbital region, and a pes with four metatarsals (although there is no indication that the pes of *M. langdoni* was tetradactyl).

Muttaburrasaurus however shows clear distinction from each of the well known iguanodontid genera. It may be distinguished from the species of *Iguanodon* by:

(1) presence of the inflated nasals,
(2) much more extensive quadratojugal,
(3) presence of the surangular boss,
(4) postorbital region of skull low and broad,
(5) maxillary teeth lacking carina,
(6) caudal centra strongly excavated ventrally, and
(7) femoral shaft more strongly curved.

It may be distinguished from *Ouranosaurus nigeriensis* by:

(1) presence of the inflated nasals, but
(2) absence of the low domes of the posterior portion of the nasals,
(3) presence of the surangular boss,
(4) maxillary teeth lacking carina,
(5) dorsal vertebrae with low to moderately, but not extremely, elevated spines,
(6) carpals not fused,
(7) anterior process of pubis less deep,
(8) femoral shaft curved,
(9) lesser trochanter placed nearly anterior to greater, and
(10) pes with four metatarsals.

It may be distinguished from *Camptosaurus* by:

(1) presence of the inflated nasals,
(2) maxillary teeth lacking carina,
(3) radius and ulna more slender,
(4) metatarsal II (and hence presumably the other metatarsals) more slender,
(5) astragalus fused with calcaneum, and
(6) low ascending process present on astragalus.

It may be distinguished from *Vectisaurus valdensis* by:

(1) posterior dorsal vertebrae with less elevated neural spines,
(2) dorsal neural spines not cleft posteromedially,
(3) posterior faces of dorsal centra only slightly concave, and
(4) indication of six, rather than five, sacral vertebrae.

It may be distinguished from *Probactrosaurus* spp. by:

(1) broad post-infratemporal bar,
(2) postorbital region of skull low and broad,
(3) anterior portion of maxilla shallow, and
(4) longer preacetabular process on ilium, and
(5) femoral shaft more strongly curved.

Photographs of a mounted skeleton of *Probactrosaurus gobiensis* in Rozhdestvenskii (1973) and Saito (1979) aided our understanding of its differences from *Muttaburrasaurus*.

There are other characteristics that also distinguish *Muttaburrasaurus* from the (well-known) iguanodontids. Except for *Camptosaurus*, none have the posteriorly sloping quadrate, nor do the others have contact between the fibula and astragalus (not included in the differential diagnosis because this is an inferred rather than observed character state). Thus it is clear that *Muttaburrasaurus* is as different from the known genera of iguanodontids as each is from the others, and is probably more distinct from most of them than *Iguanodon* is from *Probactrosaurus*. It is also clear that its greatest similarity is to *Camptosaurus*, known from western North America and western Europe (Galton, 1980).

One other form to which *Muttaburrasaurus* must be compared, if only because of the apparent similarity in maxillary tooth form, is *Mochlodon*. *Mochlodon* Seeley 1881 is almost unanimously considered a subjective synonym of *Rhabdodon* Matheron 1869 (de Lapparent & Lavocat, 1955; Romer, 1966; Steel, 1969; Olshevsky, 1978). The name *Rhabdodon* is preoccupied by Fleischmann, 1831, and hence we use the junior subjective synonym *Mochlodon*. The humerus of *Mochlodon* shows a well-developed deltopectoral crest (de Lapparent, 1947, pl. 4, fig. 9) and the lesser trochanter is less prominent (Matheron, 1869, pl. 5). Thus we feel that *Mochlodon* does not meet Dodson's criteria for an iguanodontid. *Muttaburrasaurus* clearly differs from *Mochlodon* in having strongly keeled dorsal centra, a nasal bulla, and a much higher number of maxillary teeth (18 in *Muttaburrasaurus*, 9 in *Mochlodon*). Even the crowns, although clearly similar, differ. A central carina is present on at least some maxillary crowns of *Mochlodon* (Nopcsa, 1904, pl. 2, fig. 1), and the number of

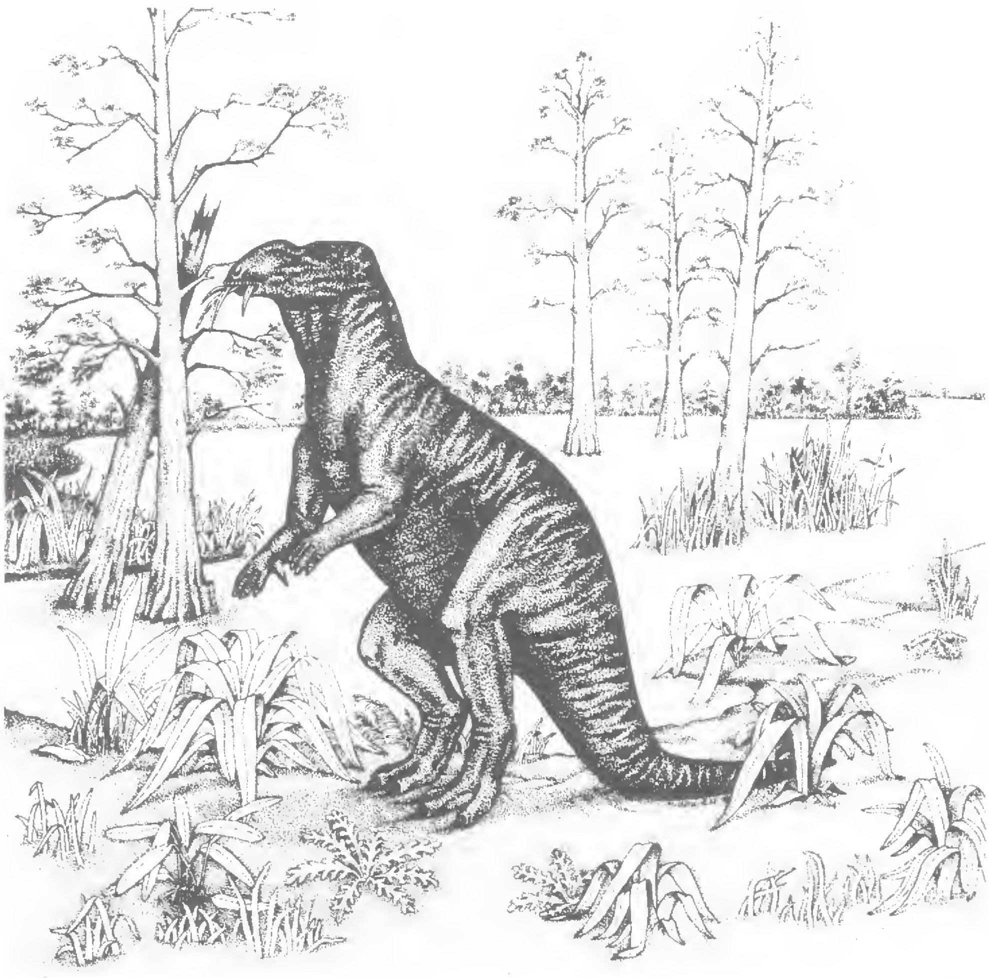

FIG. 13. Reconstruction of *Muttaburrasaurus langdoni*.

low ridges can be higher in *Mochlodon* (17 are visible on a tooth figured by Nopcsa, 1902, Taf. 2, Fig. 1). Thus one must take care in assessing relationships among ornithopods from tooth form, as has recently been stressed by Rozhdestvenskii (1977). Furthermore the radius, ulna and fibula of *Mochlodon* are much more massive than in *Muttaburrasaurus*, and the femur is curved in the transverse rather than the parasagittal plane (de Lapparent, 1947). Thus we feel that no close relationship is indicated.

Discussion

The Iguanodontidae are known from Europe, Asia, North America, Africa and now Australia (Fig. 14), from the Tithonian to the Santonian *(Craspedodon)*. They were obviously widespread, only South America not yet having yielded recognizable skeletal material. Even here there is evidence from footprints, *Camptosaurichnus* and *Iguanodonichnus* (Casamiquela and Fasola, 1968) from the Valanginian or Berriasian of Colchagua, Chile and *Sousaichnium* (Leonardi, 1976) from the Jurassic of Goias, Brazil, that iguanodontids were present. *Muttaburrasaurus* substantiates Colbert's (1973) comments on the distribution of iguanodontids into Australia.

Muttaburrasaurus is a moderately large iguanodontid, about 7 m long and 3 m high at the hips (Fig. 13). It is also one of the later iguanodontids (Table 4), and no subsequent iguanodontids are represented by specimens nearly as complete, although the contemporaneous *Probactrosaurus* is represented by reasonably complete material (Rozhdestvenskii, 1966). *Muttaburrasaurus* and *Ouranosaurus* suggest a tendency towards elaboration of the cranial skeleton in later iguanodontids, although the number of specimens is still too few to elucidate this trend. There is no indication however that *Muttaburrasaurus* was on the line toward hadrosaurs, as *Ouranosaurus* (Taquet, 1975) and *Probactrosaurus* seem to have been. Thus whatever the selective advantage of the nasal bulla of *Muttaburrasaurus*, it was presumably a parallel development to the cranial structures of the hadrosaurs.

Unlike the condition of *Camptosaurus*, *Iguanodon* and the hadrosaurs, all of the maxillary (and presumably dentary) crowns are erupted to the same degree, as if the entire dentition were replaced *en masse* rather than piecemeal. Thus there appears a single wear surface over the whole tooth row, edged with enamel laterally in the maxillary dentition, and mesially in the dentary teeth. The occlusal plane, allowing for the distortion by mesial flexion of the toothrows, appears to have been almost vertical. The plane is also straight anteroposteriorly. Ergo the dentition appears to have functioned as a pair of shears, comparable to the dentition of the ceratopsians (Ostrom, 1964). Further work on this aspect of the anatomy of *Muttaburrasaurus* must await complete exposure of the skull, but we cannot help pointing out that the unusually broad post-infratemporal bar of *Muttaburrasaurus*

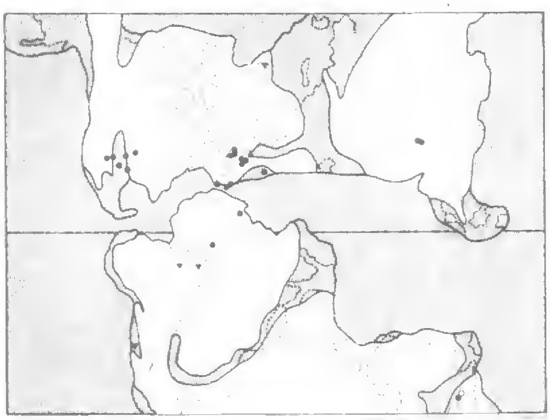

Fig. 14. Geographic distribution of iguanodontids. Solid circles indicate localities yielding iguanodontid skeletal remains: the taxa represented are those given in Table 4 plus the unstudied iguanodontid from Romania reported by Jurcsák and Popa (1978). The solid triangles represent iguanodontid tracks from regions where skeletal material has not been reported, tracks found on other continents (e.g. Asia, Europe) are not included. The open circle indicates a second iguanodontid locality near Hughenden in the Allaru Mudstone (specimen not collected). Map for the Lower Cretaceous, but Upper Jurassic and Upper Cretaceous localities included.

reflects increased volume of the adductor chamber and allows increased area of attachment for an expanded adductor mass. We can only speculate about the feeding habits, but perhaps this ornithopod was partially carnivorous.

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TABLE 4
THE DISTRIBUTION OF IGUANODONTIDS

Stage	Queensland	S. Africa	W. Africa	N. Africa	Mongolia	Iberian Peninsula	W. Europe	W. North America
Campanian								
Santonian							*Craspedodon lonzeensis*	
Coniacian								
Turonian								
Cenomanian							*Craspedodon hilli* & *Eucercosaurus tanyspondylus**	
Albian	*Muttaburrasaurus langdoni*				*Probactrosaurus alashanicus* & *Probactrosaurus gobiensis*			
Aptian			*Ouranosaurus nigeriensis*	*Ouranosaurus?* sp. #			*Iguanodon mantelli*	*Camptosaurus depressus*
Neocomian					*Iguanodon orientalis*	*Iguanodon mantelli*	*Iguanodon bernissartensis*** *Iguanodon fittoni*, *Iguanodon hollingtonensis*, *Iguanodon mantelli* & *Vectisaurus valdensis*	*Iguanodon ottingeri*
Tithonian							*Iguanodon hoggii*	
Kimmeridgian						*Camptosaurus* sp.	*Camptosaurus prestwichii*	*Camptosaurus dispar****
Oxfordian								

* Includes *Syngonosaurus macromerus*
** Also reported from this area and time are: *Iguanodon atherfieldensis, I. dawsoni, I. gracilis* and *I. seelyi*
*** Includes *Camptosaurus amplus, C. browni, C. medius* and *C. nanus*
\# cf. P. Taquet (1976), originally reported as *I. mantelli*

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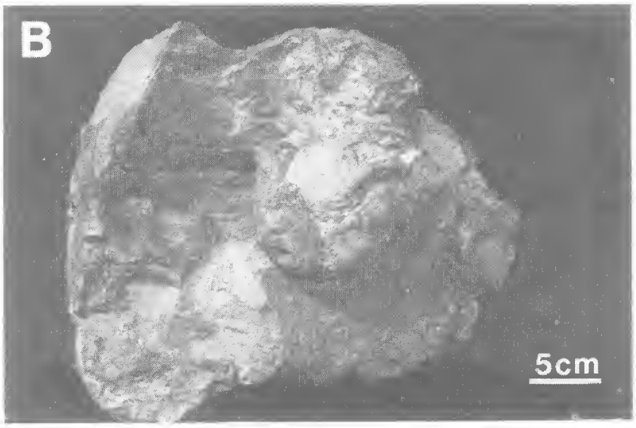
PLATE 1

The skull of *Muttaburrasaurus langdoni* (QM F6140). The scales are in cm.

A. Lateral view of skull supported by a block of plasticene.
B. Posterior view.
C. Dorsal view.


A
5cm


B
5cm

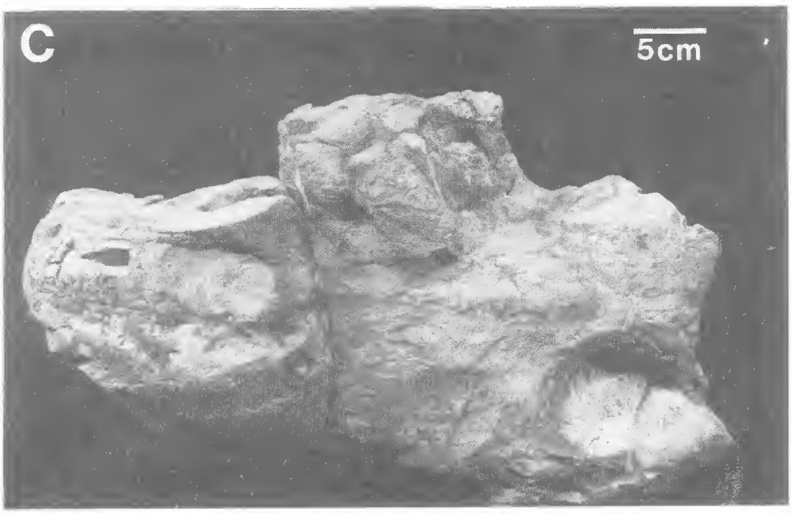

C
5cm

PLATE 2

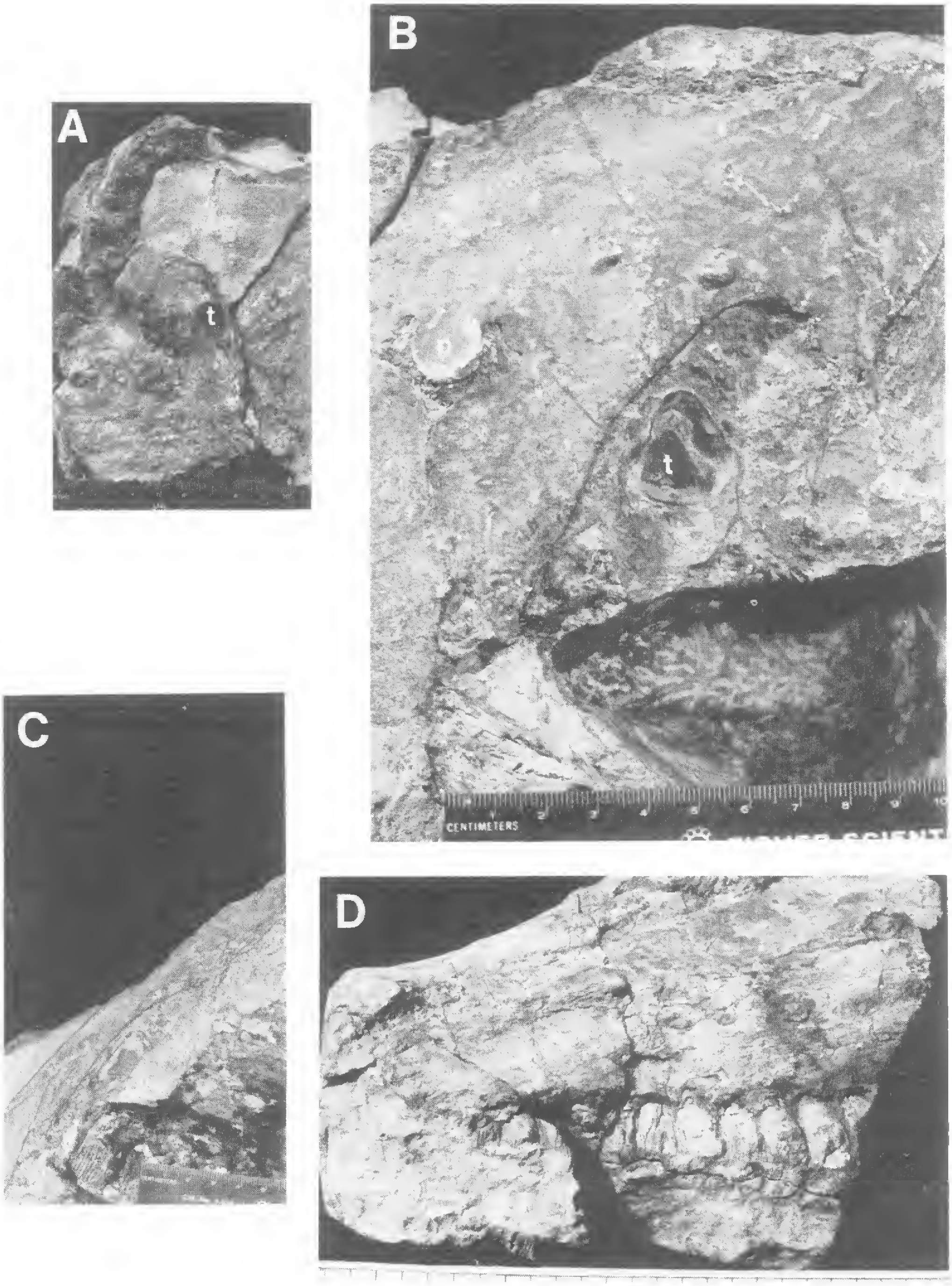
The maxillary dentition and parasphenoid of *Muttaburrasaurus langdoni* (QM F6140). The scales are in cm.

A. Break through skull (visible in Plate 1A just above the supporting plasticene) showing maxillary teeth of the right side (t) in section.

B. The same break showing maxillary teeth of the left side (t) and parasphenoid (p) in section.

C. The anteriormost maxillary crown on the left side (at lower left).

D. The left maxillary dentition in lateral view.


A
t
B
t
CENTIMETERS
C
D